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New leontiniid Notoungulata (Mammalia) from Chile and Argentina: comparative anatomy, character analysis, and phylogenetic hypotheses

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ABSTRACT

Herein we describe and name two new species of leontiniid notoungulates, one being the first known from Chile, the other from the Deseadan South American Land Mammal Age (SALMA) of Patagonia, Argentina. The Chilean leontiniid is from the lower horizons of the Cura-Mallín Formation (Tcm_1) at Laguna del Laja in the Andean Main Range of central Chile. This new species, *Colpodon antucoensis*, is distinguishable from Patagonian species of *Colpodon* by way of its smaller I2; larger I3 and P1; sharper, V-shaped snout; and squarer upper premolars. The holotype came from a horizon that is constrained below and above by $^{40}Ar/^{39}Ar$ ages of 19.53 ± 0.60 and 19.25 ± 1.22, respectively, suggesting an age of roughly 19.5 Ma, or a little older (~19.8 Ma) when corrected for a revised age of the Fish Canyon Tuff standard. Either age is slightly younger than ages reported for the Colhuehuapian SALMA fauna at the Gran Barranca. Taxa from the locality of the holotype of *C. antucoensis* are few, but they (e.g., the mylodontid sloth, *Nematherium*, and a lagostomine chinchillid) also suggest a post-Colhuehuapian

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faunal age. The second leontiniid named in this paper has been known in the literature for over 75 years as *Leontinia* sp. Several specimens referable to this species were discovered at Pico Truncado (Deseadan SALMA) during the Field Museum's first Marshall Field Expedition, led by Elmer Riggs in 1924. This "new" taxon, *Elmerriggsia fieldia*, is a small-bodied leontiniid, possessing grooved premolar protocones that lack intermediate lingual cingulae, but have well-developed labial cingulids on their lower molars. This new taxon is fairly common at Pico Truncado, in Santa Cruz, Argentina, but we have not encountered it at other localities.

The character-taxon matrix that we constructed for this analysis differs from those previously developed for notoungulates by the substantially greater number of postcranial characters used (41). *Colbertia magellanica* was used as the outgroup in all analyses. Our initial phylogenetic analysis was limited to only taxa traditionally assigned to the Toxodontia. These included a dozen taxa traditionally considered to be leontiniids, two toxodontids, four notohippids, a homalodotheriid, and two isotemnids. The taxa traditionally classified as leontiniids formed a monophyletic group, in which V-shaped muzzle, caniniform i3, femur with medial suprapatellar ridge, and large wedge-shaped fibular facet of the calcaneum were unequivocal synapomorphies. *Colpodon* spp. nested within a clade that includes the "tropical" leontiniids, *Taubatherium* and *Huilatherium.* Toxodontids and notohippids formed a monophyletic group sister to the leontiniids, with these two clades forming a more inclusive clade that previously had been called the "advanced Toxodontia." However, when five species of typotheres from three "families" were added to the analysis, the "notohippid" *Eurygenium* was identified as the nearest outgroup of leontiniids and an "advanced notohippid" plus toxodontid clade (nodes C + F). Unequivocal synapomorphies uniting these two nodes were robust calcanonavicular articulation ("reverse alternating tarsus" as evidenced by a distinct navicular facet on the calcaneum) and a distal radius with a styloid process. The presence of an entolophid fossettid in the lower molars and the downturned olecranon process of the ulna were equivocal synapomorphies for this clade. Though lacking the character states that diagnose a more exclusive "notohippid-toxodontid-leontiniid" clade, *Eurygenium* shared several unequivocal synapomorphies that unite it with these taxa. These include a well-formed fossette of upper molars formed by the posterior cingulum, absence of an entepicondylar foramen of the humerus, lack of a neck on the astragalus, a transversely elongated astragalar head, and absence of the "astragalar buttress" of the navicular.

Unconventionally, the interatheriids used in the analysis (*Federicoanaya* and *Protypotherium*, both interatheriine interatheriids) formed the sister group to the taxa traditionally considered to be the "advanced Toxodontia." Unequivocal synapomorphies uniting these interatheriids with the "advanced Toxodontia" are exclusively postcranial: tetradactyl manus, quadrate fibular facet of the calcaneum, calcaneonavicular contact (without well-formed facet on the calcaneum), and union of the groove for the tendon of the flexor hallucis longus with the astragalar trochlea. Steeply inclined ectal facets of the astragalus and calcaneum are equivocal synapomorphies (shared with *Eurygenium*, the notohippids, and toxodontids, but not leontiniids).

Inclusion of postcranial characters in the phylogenetic analysis illustrates an otherwise undetectable conflict—that of homoplasy-homology discordance between dental and postcranial characters of interatheriine interatheriids (the postcranial skeleton of "notopithicine" interatheriids [or "basal interatheriids" of Hitz et al., 2006] remain unknown). This conflict does not simply represent an arcane point, but has relevance regarding reconstructing the interrelationships of several major groups of notoungulates.

Other findings of this work include a northerly extension of the geographical range of *Colpodon* and a possible temporal extension beyond the Colhuehuapian SALMA. It appears that the fauna at Laguna del Laja is an important source of information regarding the faunal transition that occurred between Colhuehuapian and Santacrucian SALMA faunas.

FIGURE 1. Geographic setting of leontiniid localities (background map adapted from NASA image).

INTRODUCTION

Leontiniids are notoungulates characterized by their generally larger body sizes (compared to other contemporary groups of notoungulates), mesodont cheek teeth, and tendency to form caniniform to tusklike incisors (i3 and usually I2 [e.g., *Leontinia gaudryi, Ancylocoelus frequens*], but sometimes I1 [*Scarrittia* spp. and *Anayatherium* spp.]; Loomis, 1914; Chaffee, 1952; Shockey, 2005). Temporally, they ranged from the late Eocene Mustersan South American Land Mammal "Age" (SALMA) (possibly as early as the middle Eocene Barrancan "subage") to the middle Miocene, Laventan SALMA (Bond and López, 1995; Villarroel and Colwell Danis, 1997; Deraco et al., 2008). Their greatest diversity, however, occurred in the late Oligocene Deseadan SALMA. Prior to the present study, their range has been reported from southern Argentina to Colombia, and from Bolivia to eastern Brazil (fig. 1). Like nearly all notoungulates, leontiniids are known only from South America.

Leontiniids are generally considered to be the nearest outgroup to a clade of notohippids plus toxodontids, together forming a clade that Cifelli (1993) referred to as the "advanced Toxodontia." The similarity of leontiniid cheek teeth to those of homalodotheriids and some of the larger isotemnid notoungulates (e.g., *Thomashuxleya*) has suggested a relationship with these later groups, the sum of which, along with the "advanced Toxodontia," have been widely accepted as composing the more inclusive clade Toxodontia (Simpson, 1945; Cifelli, 1993; Shockey, 1997; Villarroel and Colwell Danis, 1997; Billet, 2011).

In this work, we describe and name two new leontiniid notoungulates, one the first described from Chile and the other from the Deseadan SALMA of Patagonia in Argentina. The Chilean specimen, *Colpodon antucoensis,* new species, was recovered from the lower horizons of the Cura-Mallín Formation (Tcm_1), Estero Correntoso section, early Miocene of Laguna del Laja (figs. 1 and 2) of the Andes of central Chile (Flynn et al., 2008). The new Argentine taxon, *Elmerriggsia fieldia*, has been recognized as a distinct, but unnamed species for quite some time (Patterson,

1934; Paula Couto, 1983; Shockey, 2005), but prior to our study only the upper premolars had been described (Patterson, 1934). It is from Pico Truncado, Santa Cruz province (fig. 1). We compare these two new taxa to 10 other species of leontiniids by constructing a character-taxon matrix (appendix 1) for parsimony analysis to assess the phylogenetic position of these taxa within the Leontiniidae and to test the validity of the "family" as traditionally recognized. To facilitate this analysis, we provide previously unpublished data regarding leontiniids. In particular, we describe and figure selected, phylogenetically informative postcranial elements of several leontiniids and compare these to homologous elements of *Scarrittia* and the taxon initially referred to "*Leontinia*" by Paula Couto (1983), but later named *Taubatherium paulacoutoi* by Soria and Alvarenga (1989). These postcranial data are also included in our phylogenetic analyses.

Background

Colpodon propinquus Burmeister (1885) was among the first notoungulates known. Burmeister (1885) based this taxon upon an upper molar and two lower molars found near the mouth of the Chubut River by a *naturalista viajero* ("traveling naturalist") from what was then known as the Museo Público de Buenos Aires. Burmeister regarded *Colpodon* to be morphologically intermediate between *Nesodon* Owen, 1853, and *Homalodotherium* Flower, 1873, although not in any kind of phylogenetic sense, since Burmeister believed species were anatomically fixed and immutable (Simpson, 1984). Later, the same (unnamed) traveling naturalist discovered nearly complete dentitions of *Colpodon* from the locality of the "type" specimen, which were described and figured (Burmeister, 1891: pl. 7, figs. 4–10).

The earlier paucity of notoungulate specimens ended with the fieldwork Carlos Ameghino (Simpson, 1984). Among his many discoveries in Patagonia was material that his elder brother Florentino described and named *Leontinia gaudryi* (Ameghino, 1895; the generic name was to honor Florentino's wife, Léontine [Simpson, 1984]). Although the elder Ameghino eventually described several other species of *Leontinia*, subsequent workers have regarded these as synonyms of *L. gaudryi* Ameghino, 1895, or *Ancylocoelus frequens* Ameghino, 1895 (Loomis, 1914; Patterson in an unpublished [but frequently cited] catalog; Paula Couto, 1983; Soria and Alvarenga, 1989; Shockey, 2005). Ameghino placed all these taxa within the family he named Leontiniidae Ameghino, 1895. He considered leontiniids to be related to the Homalodotheriidae, both of which he placed in the Order Ancylopoda Cope, 1889, which included the chalicotherioids (the clawed herbivorous perissodactyls of the Holarctic, which then were generally regarded as having ordinal status distinct from perissodactyls).

With considerable reluctance ("sólo de una manera absolutamente provisoria," Ameghino, 1902), Ameghino briefly regarded *Colpodon* as a leontiniid. He noted, however, that *Colpodon* also had characters reminiscent of notohippids, including the lack of labial cingulae on the incisors and a symmetric astragalus (Ameghino, 1902). Ultimately, he removed *Colpodon* from the Leontiniidae (and the more inclusive group Ancylopoda) and placed it within its own family (the Colpodontidae Ameghino, 1906). Colpodontids were included in his Order Hippoidea (Ameghino, 1906) along with notohippid notoungulates and equids. Such unions with similar South American taxa

with different Holarctic groups was internally consistent with Ameghino's strong inclination to unite South American taxa with those of the world's other continents, but at odds with the opinions of his contemporaries and later judges of relationships of South American endemics.

In contrast to Ameghino's separation of *Colpodon* from the Leontiniidae, Gaudry (1906) believed that there was a close relationship between *Colpodon* and Deseadan leontiniids. Indeed, he lumped the Deseadan taxa *Leontinia gaudryi* and *Ancylocoelus frequens* within *Colpodon*.

Early to middle 20th-century students of South American ungulates (e.g., Patterson, 1934; Simpson, 1945) did not follow Gaudry's system of placing the Deseadan leontiniids within *Colpodon*, but regarded the Colhuehuapian (early Miocene) species of *Colpodon* as generically distinct from the Deseadan taxa, yet still leontiniids. However, its generally notohippidlike incisors continued to cause doubts in others about its leontiniid affinities. Soria and Bond (1988), for example, referred *Colpodon* to the Notohippidae. Their findings evidently influenced the placement of *Colpodon* within the Notohippidae in the authoritative classification of McKenna and Bell (1997). By that time, however, Bond and López (1995) had already returned *Colpodon* to the Leontiniidae based on the discovery of a specimen possessing labial cingulae on the incisors.

Cifelli (1993) performed the first cladistic phylogenetic analysis that included *Colpodon*. He indicated that his initial analysis placed *Colpodon* as the sister taxon to a clade that included leontiniids, notohippids, and toxodontids, but in the final analysis, in which "ancestral states were defined" (Cifelli, 1993: 206), *Colpodon* nested within the Leontiniidae. Indeed, in that

FIGURE 2. Photograph of exposures of the Cura-Mallín Formation at the Laguna del Laja, Miocene, Chile.

modified analysis, *Colpodon* was sister to *Ancylocoelus*, with the loss of the canine regarded as the synapomorphy linking these two leontiniids. Similar results using outgroup comparisons were reported in Villarroel and Colwell Danis (1997) and Shockey (2005).

To date, the most comprehensive phylogenetic study of the Leontiniidae was that of Villarroel and Colwell Danis (1997). Their character-taxon matrix for the first cladistic phylogenetic analysis designed to elucidate the evolutionary relationships among leontiniids originated as a descriptive table in the master's thesis of the second author (Colwell, 1965), although it was not originally designed for phylogenetic analyses. That matrix was small enough that the authors were able to perform an exhaustive search for the shortest tree, yielding a phylogeny suggesting that leontiniids formed two major clades: a "tropical clade" including the low latitude *Taubatherium* and *Huilatherium* and the remaining "Patagonian" leontiniids. Shockey (2005) added two new taxa from Salla (*Anayatherium ekecoa* and *A. fortis*) to the matrix and performed an exhaustive search that suggested that the midlatitude Salla leontiniids nested among the "Patagonian" clade.

The studies by Villarroel and Colwell Danis (1997) and Shockey (2005) were based exclusively on dental characters, and included some species level ambiguities since scoring was at the generic level. For example, there is enough variability between *Taubatherium paulacoutoi* and *T. major* that a composite score for the genus is problematic (see Results and Discussion).

For the current study, leontiniid taxa were evaluated at the species level. For clarity, and to reduce the possibility of ambiguities, the individual specimens studied or specific published descriptions are documented (appendix 2). Moreover, illustrations (figs. 2 and 5–12) of several of the characters and their states are provided to facilitate replication of our observations and analyses. Characters in this study differ from all previous analyses by including features of both the dentition and the postcranial skeleton.

Major goals of this study are to: (1) document and describe two new species of leontiniids from southern South America (Chile and Argentina); (2) place these species (as well as the Leontiniidae clade) within the context of an explicit phylogenetic hypothesis; and (3) attempt to resolve the phylogeny of taxa frequently associated with the Leontiniidae but that have been problematic historically (e.g., *Colpodon* and the Homalodotheriidae).

Materials, Abbreviations, and Methods

Materials. The initial stimulus for this paper is the analysis of a recently discovered leontiniid from the Laguna del Laja area of the central Chilean Andes, SGOPV 5704, herein designated as the holotype of *Colpodon antucoensis*, new species (fig. 3). It is curated in the fossil vertebrate collection (SGOPV) of the Museo Nacional de Historia Natural, Santiago, Chile. We also describe and name a second new taxon that has been discussed in the literature for some time as "*Leontinia* sp." (Patterson, 1934; Paula Couto, 1983; Shockey, 2005). This new taxon, *Elmerriggsia fieldia*, is from Pico Truncado, southern Patagonia (Santa Cruz, Argentina). Other specimens from which data were obtained, and publications we used for scoring characters, are listed in appendix 2.

Abbreviations. Institutions (with abbreviations used in the text) that provided access to

our study of notoungulates include the American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH and specimen prefixes of P or PM); the Florida Museum of Natural History, University of Florida, Gainesville (FLMNH and specimen prefixes of UF).

The "number" sign (#) is used throughout to indicate a specific character as listed by number in the character analyses. The number parenthetically associated with # represents the character state.

I, C, P, and M represent upper incisors, canines, premolars and molars, respectively (lower case notation for lower teeth). Terminology for dental characters generally follows that of Patterson (1934). Many of these terms are graphically represented and defined in figures 3, 5, 6, and 9 (postcranial characters are given in figs. 7, 8, 10, 11, and 12). We follow Smith and Dodson (2003) for orientation of dentitions, where the four cardinal directions are mesial, distal, lingual, and labial. Thus, for example, the anterolingual cingulum of previous workers will be denoted as the mesiolingual cingulum, etc. Mesiodistal dimensions (lengths) of teeth were obtained at the greatest length of the ectoloph. Transverse dimensions (widths) of cheek teeth were measured from the base of the paracone ridge of the ectoloph to the internal border lingual to the protoloph, including any cingulae.

Methods: Parsimony analyses were performed in PAUP 4.0b10 (Swofford, 2000), using a heuristic search. All characters were treated as unordered and of equal weight. The character-by-taxon matrices include up to 27 species of notoungulates (12 of which are leontiniids) and 83 dental plus postcranial characters. To elucidate the phylogenetic position of leontiniids within toxodontian notoungulates, we included taxa from a variety of toxodontian "families" (e.g., toxodontids, notohippids, isotemnids, and a homalodotheriid). Taxa were selected based on the presence of reasonably complete dental and postcranial material. Our desire to undertake a more comprehensive analysis that includes postcranial elements limited selection to mostly post-Eocene taxa, since pre-Oligocene notoungulate skeletons are scarce. Sufficient material was available, however, to include the Eocene isotemnids *Thomashuxleya* and *Anisotemnus* and the Paleocene-Eocene oldfieldthomasiid, *Colbertia magellanica*. *Colbertia* served as the outgroup for the cladistic analyses. A second analysis was performed in which five typothere taxa were added (see appendix 2).

The age of the *Colpodon antucoensis* holotype was estimated from radioisotopic analyses of two ashfall tuff samples (CH-31 and CH-32; fig. 4; appendix 3) that bracket the horizon at Estero Correntoso of Laguna del Laja from which the holotype was discovered. The sample ages were determined by the $^{40}Ar/^{39}Ar$ incremental heating method at the University of California Santa Barbara Laboratory for Argon Geochronology using the general procedures and system described by Gans (1997). Standard density and magnetic separation techniques were used to generate pure separates of plagioclase from these ash layers. Taylor Creek Rhyolite sanidine with an assigned age of 27.92 Ma was used as the flux monitor. For comparison, we obtain an age of 27.75 Ma on Fish Canyon Tuff sanidine (another widely used standard). The results of these analyses are given in the "Distribution" section of the description of *C. antucoensis* (below).

SYSTEMATIC PALEONTOLOGY

NOTOUNGULATA Roth, 1903

TOXODONTIA Owen, 1853

LEONTINIIDAE Ameghino, 1895

COLPODON Burmeister, 1885

Colpodon antucoensis, new species

Figure 3, table 1

SYNONYMY: "Leontiniidae, unident.," Flynn et al., 2008: table 1, fig. 4e.

HOLOTYPE: SGOPV 5704 includes a nearly complete upper dentition, of which the left dental series has been exposed (the right series remains embedded in the extremely hard volcaniclastic matrix). Aside from the premaxillary and maxillary regions around the roots of the teeth, no bone was preserved.

DISTRIBUTION AND AGE: Known only from the type locality, Estero Correntoso, near Laguna del Laja, in the Andes of central Chile. The holotype was found in the lower exposures of the Cura-Mallín Formation (Tcm_1), which are composed of volcaniclastic sandstone, mudstone, and granule conglomerates (Herriot, 2006; Flynn et al., 2008). Two ashes (CH-31 and CH-32; table 2) bracket the fossil-bearing horizon. Both samples yielded somewhat disturbed age spectra, with low temperature, fairly flat segments ("pseudo-plateaus") with apparent ages of ~20–21 Ma, climbing to somewhat older ages (23–24 Ma) at higher temperatures (fig. 4). This type of behavior is reasonably common in volcanic plagioclase separates that have experienced low levels of hydrothermal alteration, and may indicate that the more retentive sites in the plagioclase incorporated minor amounts of excess argon during hydrothermal alteration. However, both samples yield well-behaved inverse isochrons, with estimated ages of 19.25 ± 1.22 for the stratigraphically higher CH-31 and 19.53 ±0.60 for the lower CH-32 (fig. 4, table 2, appendix 3) as well as a trapped argon component with a somewhat elevated $^{40}Ar/^{36}Ar$ ratio of 340:360. Both samples are easily within analytical uncertainty of each other and suggest the fossil age is ~19.5 Ma. It should be emphasized that this age is relative to our assigned flux monitor (Taylor Creek Rhyolite) age of 27.92 Ma as reported by Dalrymple and Duffield (1988). If the age of our flux monitor is revised to an older age in order to make it compatible with a Fish Canyon Tuff age of ~28.2 Ma (e.g., Renne et al., 2010), then the estimated age of the ash layers would be increased slightly to ~19.8 Ma.

ETYMOLOGY: The specific name, *antucoensis*, is in reference to Antuco, a snow-capped stratovolano (2979 m) overlooking Laguna del Laja and the fossil localities of the region (fig. 2). The name emphasizes the role volcaniclastics played in preserving dentitions (although apparently destroying bone in some cases) at Laguna del Laja and other Cenozoic localities of the central Andean Main Range of Chile.

DIAGNOSIS: Since only the upper dentition of *Colpodon antucoensis* is known, the diagnosis necessarily can include only upper tooth characters. It is a relatively small (about tapir-sized) member of the Leontiniidae, sharing many of the general features as well as a couple of synapomorphic traits characteristic of the family (see Node A of Results). These include the strong anterior convergence of the dentition resulting in the muzzle having a V-shape in occlusal view

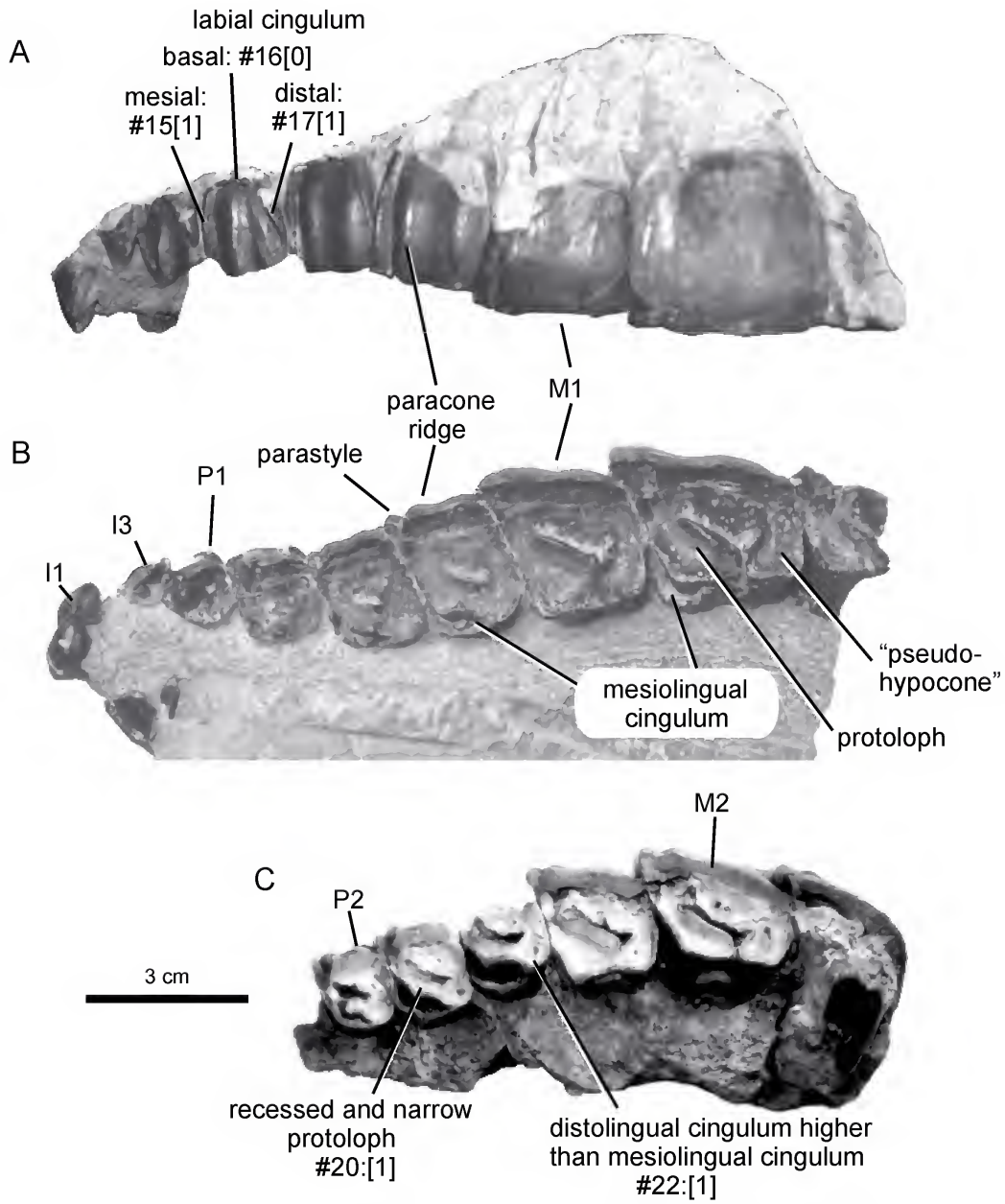


FIGURE 3. Left dentitions of *Colpodon* spp.: *Colpodon antucoensis,* new species (SGOPV 5704) in lateral (**A**) and occlusal (**B**) views; **C,** *Colpodon propinquus* (FMNH P 13310) in occlusal view. The numbers below the descriptors indicate character number (#) and state (see Character Analysis). Scale bar applies to all.

(#1[1] of analysis) and mesodont dentition (#12[1]). *Colpodon antucoensis* differs from most leontiniids in the absence of an enlarged, caniniform upper incisor, very small or absent I2, and I3 having the greatest mesiodistal dimension of the upper incisors.

Colpodon antucoensis is similar to *C. propinquus* (and lectotype of *C. distinctus*) in: general size; the absence of upper canine (#2[1]); and relatively small and recessed premolar protoloph

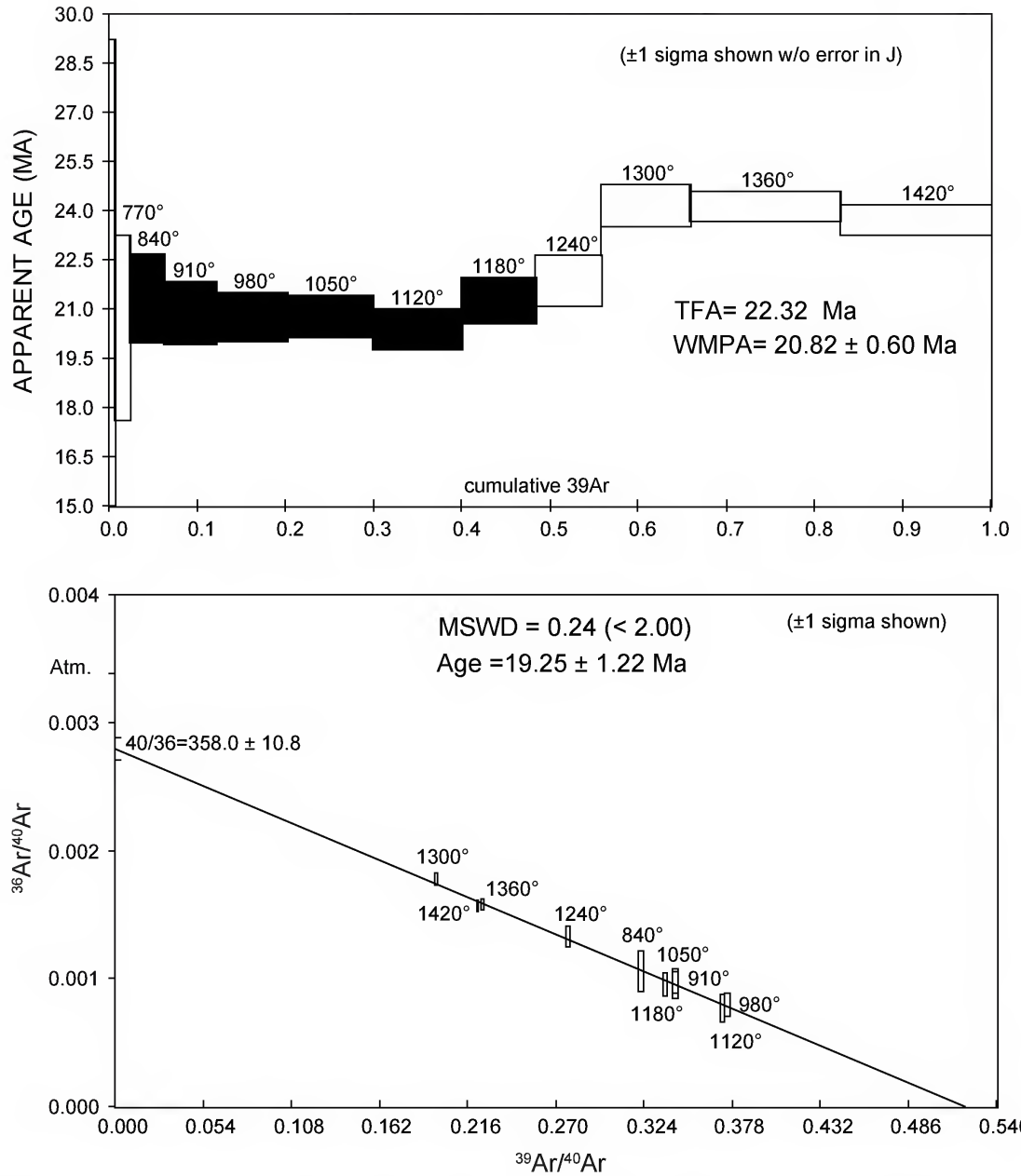
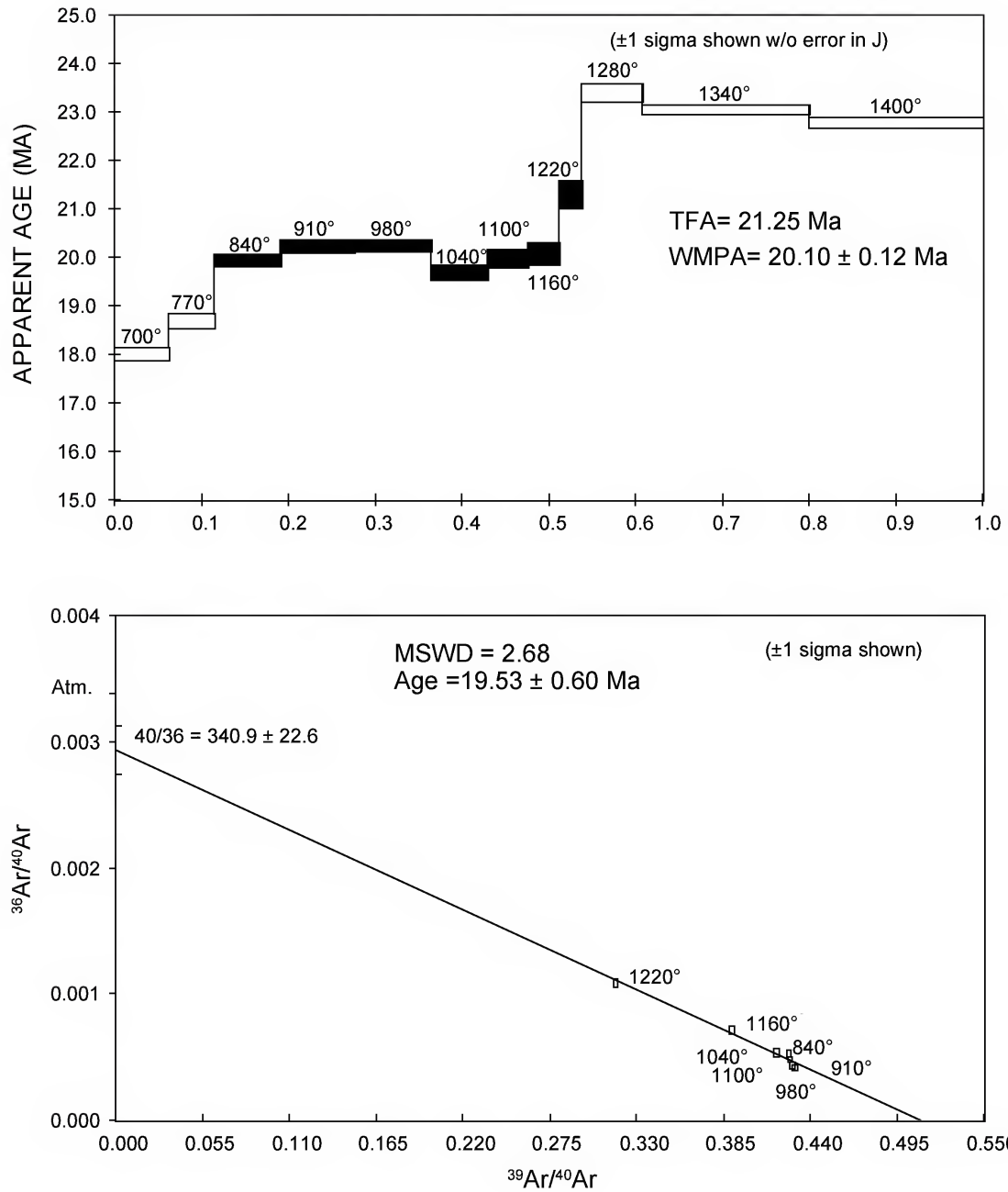


FIGURE 4. $^{40}Ar/^{39}Ar$ age spectra and inverse isochron plots for samples CH-31 (above) and CH-32 (opposite page). Age spectra illustrate apparent age versus cumulative fraction of ^{39}Ar released. Shaded boxes indicate steps used to calculate weighted mean plateau ages. Plotting these steps suggests that most of them fall on simple isochrons with a $^{40}Ar/^{36}Ar$ ratio of the trapped component somewhat higher than atmospheric gas, giving a more reliable estimate of the ages at ~19.5 Ma, or ~19.8 Ma when corrected for a revised age of the Fish Canyon Tuff standard.



that does not unite with the mesiolingual cingulum (except with extreme tooth wear)(#19[1]). *Colpodon antucoensis* is distinct from *C. propinquus* (and lectotype of *C. distinctus*) by way of its more pointed (V-shaped) snout; smaller I1; much smaller I2 (I2 is largest incisor in lectotype of *C. distinctus*); larger I3, larger and fully premolariform P1; and straight rather than curved lingual border of mesiolingual cingulum.

The cheektooth row of *Colpodon antucoensis* is similar in length to that of *Ancylocoelus fre-*

quens (e.g., P 13479); however, the total length of the palate is less, owing to the short anterior region of the snout of *C. antucoensis*. *Colpodon antucoensis* differs from *Ancylocoelus* in its sharper, more labially projecting upper premolar parastyle, which forms a mesiolabial cingulum in *Colpodon antucoensis*; presence of posterior longitudinal labial cingulum of upper premolars (absent in *Ancylocoelus*); protoloph of premolar more labial relative to distolingual bulge formed by distolingual cingulum leaving a gap between the body of the protoloph and mesiolingual cingulum; paracone ridge of M1–2 of *Colpodon antucoensis* is shallower than that of *A. frequens*; lingual cingulum of M1–2 not as large or as bulbous as that of *A. frequens*; upper molar cristae indistinct, resulting in absence of the forked fossette seen in *A. frequens*, wherein the anterior fossette is divided by the first crista, and in some specimens by the second crista.

Description: Although most of the exposed teeth are well preserved, little else remains of the specimen. The only bone preserved is that which contains roots of the upper teeth, part of the premaxilla and parts of both left and right maxillae. The teeth are fully erupted and show considerable wear.

Only the tips of both I1s are present. These clearly indicate that the I1 is not enlarged, as in *Scarrittia* and *Anayatherium* spp., but is small, even compared to the small I1s of *C. propinquus* and *Ancylocoelus*. The labial enamel is flat, lacking any signs of longitudinal crests or undulations. There is no evidence of a cingulum, but since the base of the tooth was not preserved its absence cannot be asserted with confidence.

There is a small gap between I1 and I3. If a tooth had been present in life, it would have been smaller than I1 and much smaller than the I2 of other known specimens of *Colpodon*.

The second incisor preserved on the specimen is judged to be an I3 since there is a gap between it and the I1 on both sides and it unambiguously occurs in the premaxilla (the premaxilla-maxillary suture is visible on the dorsal side of the specimen). The I3 is transversely narrow, thus its ectoloph forms the long axis of the tooth, which lies obliquely to the sagittal plane. Anterior occlusal wear results in the tooth having a blunt point, suggestive of occlusion with a hypertrophied i3. The lingual side of the ectoloph has numerous vertical striations, indicating that numerous cuspules form the unworn ectoloph, as previously demonstrated for the molar ectoloph of *Leontinia* (Patterson, 1934). A labial cingulum lies at the base of the tooth, as it does on the premolars. The tooth has a single robust root that shows some posterior curvature as it enters the bone. However, little of it or the roots of the cheek teeth are preserved, other than the cross section visible just dorsal to the level of the basal enamel.

P1 also appears to be single rooted, despite the fact that its labiolingal dimension is much greater than that of the I3 in this specimen, or the P1 of other known specimens of *Colpodon*, which tend to be more incisiform (see Burmeister, 1890: pl. VII, fig. 4). The mesiolingual portion of the tooth is heavily pitted and bordered by a thin cingulum that extends to the labial side of the tooth, where it grades into a distinctive parastyle that forms a sharp, vertical ridge on the mesiolabial border of the tooth. This parastyle lies lingual to the paracone, thus the ectoloph connecting the two is nearly perpendicular to the sagittal plane. The paracone ridge is sharply convex at the crown, but lies lower on the ectoloph at the dorsal base of the tooth than it does at the occlusal level. Although damage obscures details of the anterior labial cingulum, the cingulum

Table 1. Measurements (mm) of upper dentition of SGOPV 5704, holotype of *Colpodon antucoensis*, new species.

Tooth	Mesiodistal	Labiolingual
I1	8.7	—
I2	—	—
I3	11.2	7.7
P1	12.9	12.2
P2	14.1	15.8
P3	16.0	20.9
P4	17.9	26.0
M1	26.5	29.1
M2	32.4	30.3

sharply defines the posterior base of the tooth, as well as the posterolabial border.

The mesiodistal dimension (anteroposterior dimension) of P2 is similar to the transverse dimension, giving the tooth a quadrate shape in occlusal view. The flat lingual border of the mesiolingual cingulum adds to the impression of a squared tooth (in occlusal view). Undulations of the ectoloph are limited to the ridges of the parastyle, paracone ridge, and posterior cingulum, as well as a deep sulcus between the parastyle and paracone ridge. The metacone ridge is an inconspicuous, broad, low convexity. The parastyle forms a continuous enamel wall that runs to the dorsal margin of the tooth, grading into the labial cingulum, which in turn grades into a well-defined distolabial cingulum. P2 has a protoloph, but it is small and has a vertical lingual wall that does not grade into the mesiolingual cingulum. Unlike *Leontinia, Anayatherium* spp., *Elmerriggsia, Huilatherium*, and *Homalodotherium*, there is no ridge connecting the protoloph to the mesiolingual cingulum, thus the basin defined by the cingulum is undivided (a "simple Leontiniid basin" of Villarroel and Colwell Danis, 1997). Such a divided basin also is absent in all specimens of *Colpodon* that we observed, except that in *C. propinquus* figured by Burmeister (1890: pl. VII, fig. 4). The protoloph of P2 of *Colpodon antucoensis* is thin and encloses a moderately large fossette. The distolingual corner of the tooth is lower than the highest point of the protoloph and is likely the homolog of the posterior cingulum of other leontiniids (see Patterson, 1934). This distolingual cingulum does not bulge medially beyond the lingual level of the protoloph as it does in P3–4.

The P2–4 of *Colpodon antucoensis* all have the same general form as the equivalent premolars of *Colpodon propinquus* (fig. 3; Patterson, 1934: fig. 11b). The most striking similarity is the form of their protolophs. In *Colpodon antucoensis* and *C. propinquus*, as well as specimens referred to *C. distinctus*, the P2–4 protolophs have a vertical lingual border that is recessed labially from the lingual border of the tooth, yielding a gap between the protoloph and the mesiolingual cingulum. The posterior cingulum defines the lingual border of the posterior cusp, which has a greater occlusal area than the protoloph. This structure gives the distolingual regions of P3–4 a bulging appearance. The distolabial cingulae of P2–3 of *Colpodon antucoensis* are large and sharply

Table 2. Summary of $^{39}Ar/^{40}Ar$ analyses.

Sample ID	**04PGCH-31**	**04PGCH-32**
Irrad #	SB55-032	SB55-033
Mineral	Plagioclase	Plagioclase
Geological context	Estero Campamento – 1 m thick ash fall deposit	Estero Campamento – 1 m thick pumice fall, ~ 50 m below CH-31 – xtl-rich, juvenile
Experiment	12 step heat	12 step heat
Prefer age(Ma)	19.25	19.53
± 2 sigma (Ma)	1.22	0.60
TFA	22.32	21.25
WMPA	20.82 ± 60	20.1 ± 0.12
WMPA temp steps (% 39)	840-1180°(44%)	840°–1220°(42%)
Isochron age	19.25 ± 1.22	19.53 ± 0.6
Iso age temp steps (% 39)	840°–1420°(98%)	840°–1220°(42%)
MSWD	0.24	2.68
40/36i	358 ± 5.3	340.9 ± 22.6
K/Ca	0.015–0.019	0.065–0.088
Rad (%)	47–77	60–87.5
Comments on geochron	Climbing spectrum, with both low and high T "pseudoplataeu") – more reliable isochron	Climbing, irregular spectrum with low T "pseudoplateau" – more reliable isochron

defined. These are absent on P2–3 of our comparative specimen of *C. propinquus* (P 13310), but this is apparently variable in *Colpodon* since they are present on P2–3 of other specimens (P 13304).

The sheared dorsal surface of the holotype provides some cross sectional information regarding the roots. The incisors and P1 have single roots. P2 root form is ambiguous. However, P3 and P4 show a pattern of fusion among three roots similar to that noted by Ameghino in his description of the type of *C. distinctus* (Ameghino, 1902). On the holotype of *C. antucoensis*, the natural cross section illustrates that the anterolabial and posterolabial ("paracone" and "metacone") roots are fused to one another, as are the posterolabial and lingual ("protocone") roots of P3. On P4 the lingual and posterolabial roots form a single transverse crest, separate from a distinct anterolingual root.

Nearly all other differences in the upper premolars of the holotype of *Colpodon antucoensis* and comparative specimens of other species of *Colpodon* may be explained most simply by differences in tooth wear. For example, the holotype of *Colpodon antucoensis* lacks the shallow enamelless pits seen in the posterior regions in the little-worn dentition of *Colpodon propinquus* (fig. 3C); however, with greater wear such pits in the holotype, if they existed, also would have been obliterated.

The molars of *Colpodon antucoensis* resemble those of *Colpodon propinquus*. In both taxa,

the M1 has worn to a level where the protoloph is united to the "pseudohypocone," thus isolating the major fossette. M2 also has nearly worn to this level; a shallow lingual enamel-lined opening remains, but it would have disappeared with a few more millimeters of wear. M3 is fully erupted, but only the protoloph and part of the ectoloph are preserved.

With its modest wear and good preservation, M2 preserves many informative characters. Its ectoloph forms smooth undulations over its low parastyle, paracone, and metacone ridges. Neither M2 nor M1 have any labial cingulae. The internal valley, soon to be isolated as a fossette with additional wear, lacks any of the distinctive branches seen in *Ancylocoelus* or *C. propinquus*, but these too are often lacking in worn specimens of those other taxa. There are no minor fossettes lingual to the ectoloph, as in some specimens of *C. propinquus* (e.g., P 13310: fig. 3C). A mesiolingual cingulum extends along the base of the protoloph, but not to the "pseudohypocone."

Comments: *Colpodon antucoensis* is most distinct from *C. propinquus* and specimens referred to *C. distinctus* in its anterior dentition (I1 to P1). I1 in *C. antucoensis* is smaller and has a simpler morphology. The space between I1 and I3 is so small that had it contained an I2 it would have been very small, much smaller than the I2 of *C. propinquus* and specimens referred to *C. distinctus*. The tip of the snout bearing these small anterior incisors in *C. antucoensis* is likewise small, coming to a sharper point than in other specimens referred to *Colpodon*. But whereas I1 and I2 are small, I3 is larger than in other known specimens of *Colpodon*, in which the I3 is the smallest incisor. The diminutive tip of the snout, small anterior incisors and larger I3 are likely apomorphic compared to other leontiniids, including other species of *Colpodon*.

Elmerriggsia fieldia, new taxon

Figures 5, 6, 7; table 3

Synonymy: *Leontinia* sp. Patterson, 1934: fig. 10c; Paula Couto, 1983: fig. 3d; and Shockey, 2005: fig 1.

Holotype: FMNH P 13386, upper maxillary fragment with P2–M2, from Pico Truncado.

Referred Material: All referred specimens are from the FMNH collections and were collected by Elmer Riggs at Pico Truncado. They include: P 13379, right I2, I3, and C, with an associated premolar, probably a P2 (though it had been originally reconstructed on the specimen in a manner that erroneously suggested it was a P1); PM 61101, right P1–P3, in a maxillary fragment that contains the posterior half of the alveolus for the canine; P 15060, right unworn P3; PM 61102, right M1; P 13501, nearly complete jaw with both hemimandibles and the complete dentition, missing just the left i1, and right i3, and p1; P 13384, left mandibular fragment with p4–m3; P 13510, mandibular symphysis with anterior right ramus and p3–m1; P 13627, left mandibular fragment with m2–3 and associated right m3; P 13502, right mandible with p2–m3; PM 412 (F 250), right unciform; PM 411 (field number F 250), right lunar; PM 410 (F250), ungual phalanx; PM 413 (F 700), right calcaneum; and PM 415 (F 700), right astragalus. P 13632, left distal femur and left proximal tibia-fibula, is tentatively referred to *Elmerriggsia*, but since some fragmentary dental material from Pico Truncado may be referred to *Leontinia gaudryi*, it is possible that P 13632 pertains to that taxon instead.

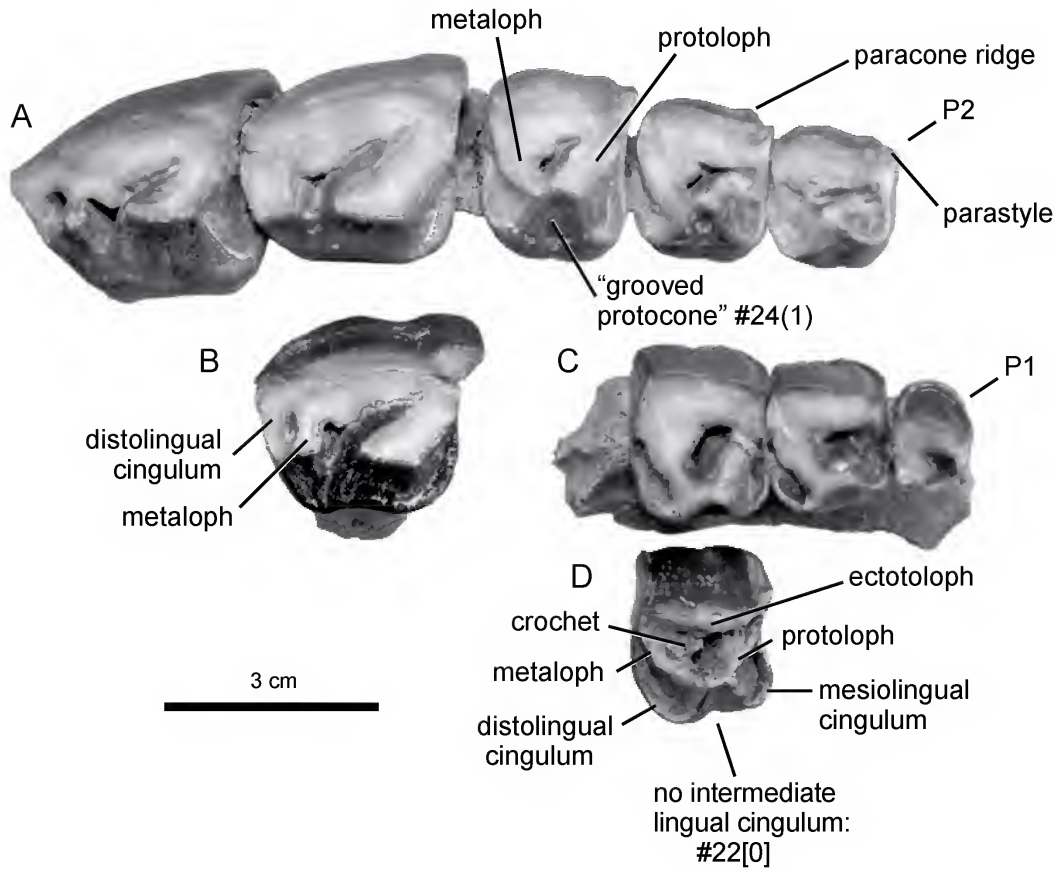


FIGURE 5. Upper cheek teeth of *Elmerriggsia fieldia*, new taxon. **A,** P 13386, holotype, P2–M2; **B,** PM 61102, right M1; **C,** PM 61101, right P1–P3; and **D,** P 15060, unworn, right P3. Scale bar applies to all.

Distribution and Age: Deseadan (late Oligocene) SALMA of Patagonia. The specimens herein assigned to the new taxon *Elmerriggsia fieldia* were discovered at Pico Truncado (Departamento de Santa Cruz) during the first Marshall Field Expedition to South America in May 1924. Pico Truncado is Deseadan in age, radioisotopically constrained between about 27 and 29 Ma (Flynn and Swisher, 1995).

Etymology: *Elmerriggsia* for Elmer S. Riggs, in honor of his leadership of the Marshall Field Expeditions to South America and *fieldia* in honor of the Marshall Field Expeditions and the Field Museum of Natural History. The holotype and referred specimens were discovered during the first Marshall Field Expedition to South America in 1924.

Diagnosis: Relatively small leontiniid, having grooved premolar protocones that lack intermediate lingual cingulae but have well-developed labial cingulids on the lower molars. Referable to the Leontiniidae by sharing many of the general features and synapomorphic traits with other members of the family. These include, V-shaped snout appearance in palatal view (#1[0]; inferred from P 13379); caniniform pair of upper incisors (#3[2]); mesodont dentition (#12[1]); i3 caniniform (#32[1]); cingulid distinct and continuous on lingual side of lower

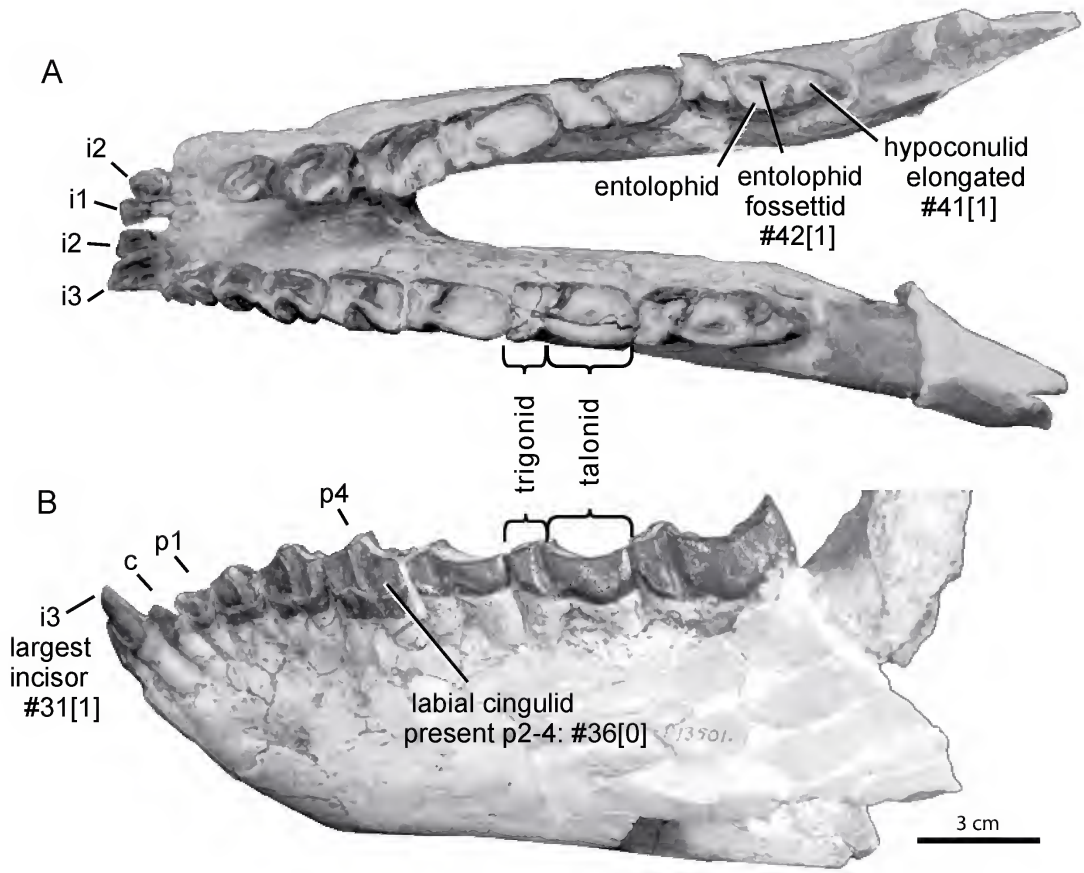


FIGURE 6. Mandible of *Elmerriggsia fieldia* (FMNH P 13501) in occlusal (**A**) and lateral (**B**) views.

premolars (#35[1]); large fibular facet of calcaneum (#74[2]); fibular facet having greater proximal transverse dimension than distal (#75[2]); proximal tarsus of "advanced Toxodontia" but with ectal facets that are not steeply inclined (#76[0]). *Elmerriggsia* is distinguishable from all other leontiniids by absence of a connecting intermediate lingual cingulum of the upper premolars, although it has well-developed mesio- and distolingual cingulae on P2–4.

Differs from *Leontinia gaudryi* by its much smaller size, absence of the intermediate lingual cingulum of P2–4, upper premolar occlusal surfaces subquadrate (rather than transversely deep as in *L. gaudryi*), and with smoother molar and premolar ectolophs.

Differs from *Scarrittia canquelensis* by its much smaller size, absence of the intermediate lingual cingulum of P2–4, squarer premolar protolophs, and relatively deeper mandible (maximum depth of mandible at the posterior region of m3 is 45% the length of i1 to m3 in *Elmerriggsia*, but only about 35% in *S. canquelensis*). Differs from *S. barranquensis* by its smaller size, squarer upper premolars (transverse dimensions subequal to mesiodistal, not transversely deeper), lacking bulbous distolingual premolar bulge, and having squarer premolar protolophs.

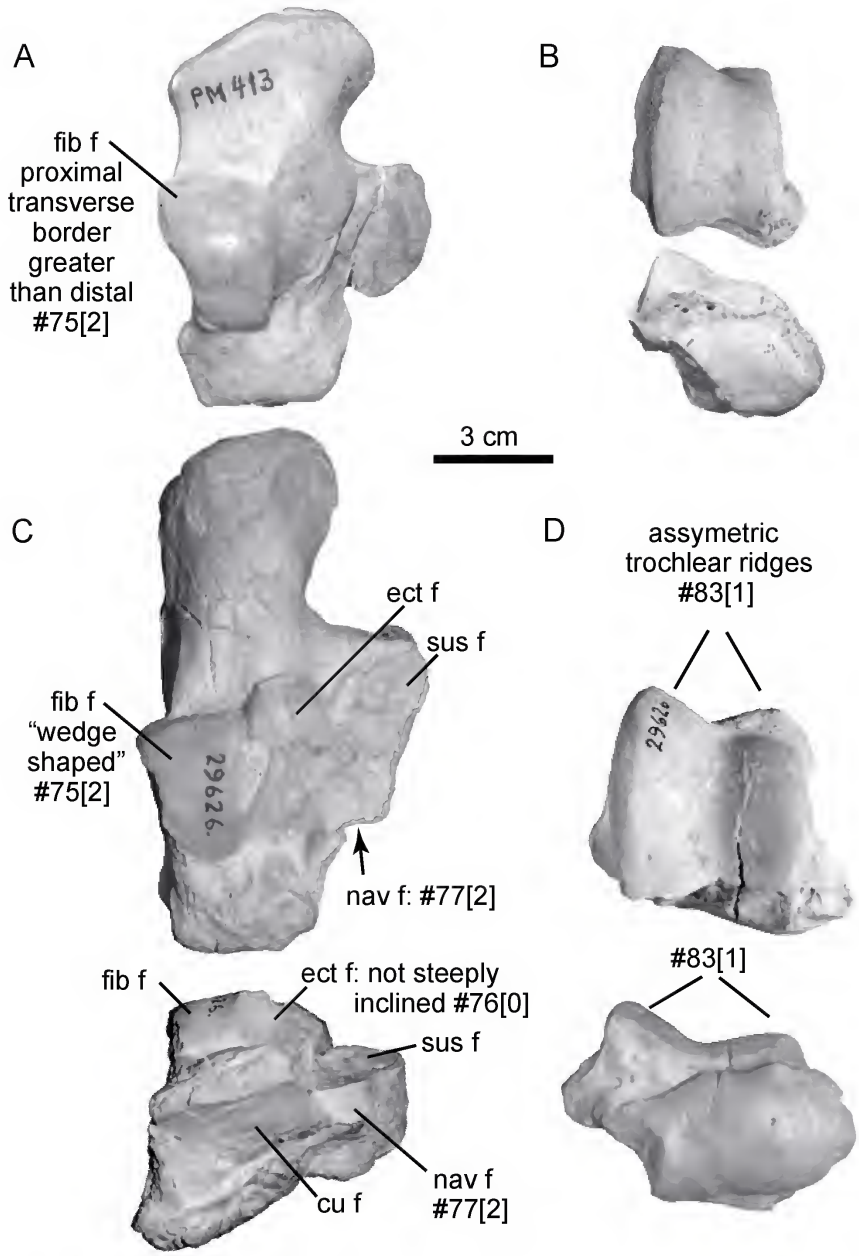


FIGURE 7. Proximal (right) tarsals of leontiniids. **A,** calcaneum of cf. *Elmerriggsia fieldia* (PM 413); **B,** astragalus of cf. *Elmerriggsia fieldia* (PM 415); **C,** calcaneum of *Scarrittia canquelensis* (AMNH 29626), in dorsal and distal views; and **D,** astragalus of *Scarrittia canquelensis* (AMNH 29626), in dorsal and distal views. Abbreviations: cu, cuboid; ect, ectal; f, facet; fib, fibula; nav, navicular; sus, sustentacular.

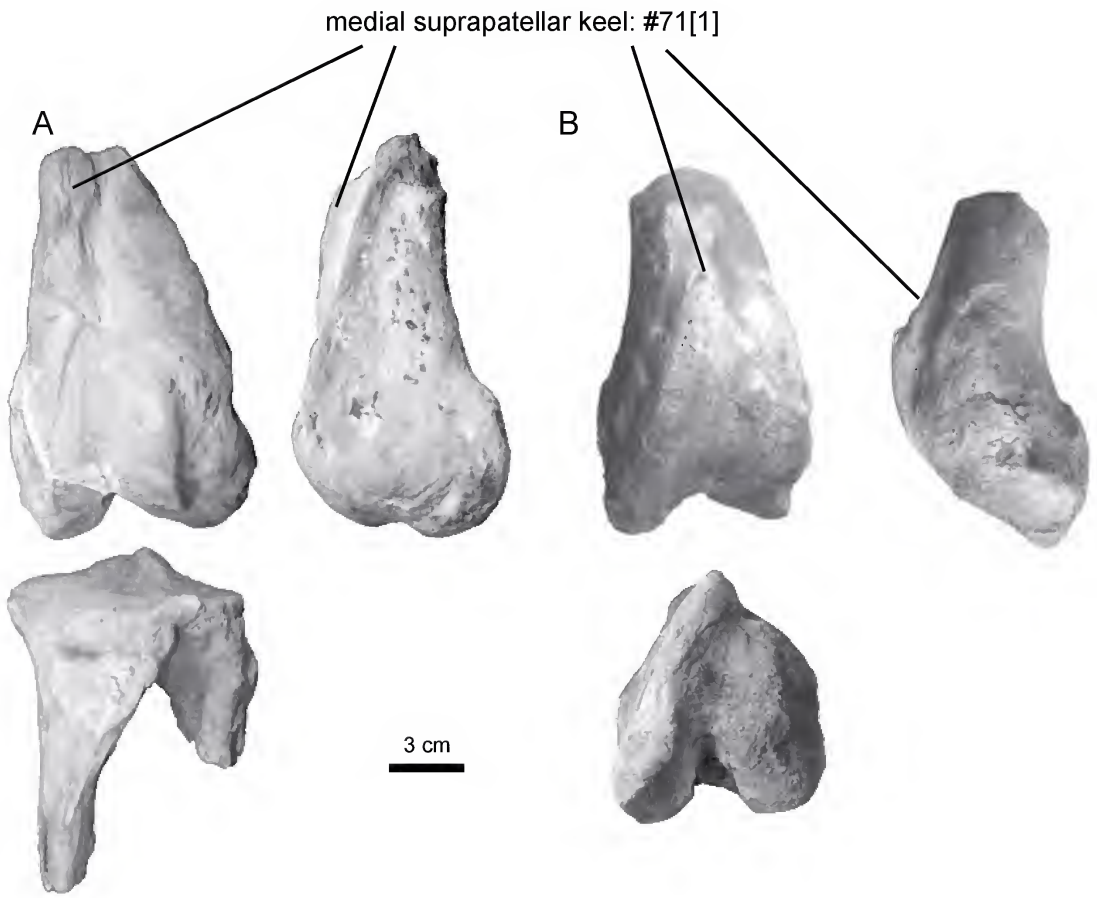


FIGURE 8. Knee region of leontiniids. **A,** left distal femur and proximal tibia-fibula (P 13632) in dorsal and lateral views of c.f. *Elmerriggsia fieldia*; and **B,** right (reversed to show as left) distal, femur of *Anayatherium*, cf. *A. fortis* in dorsal, lateral and distal views. Scale bar applies to all.

Similar in size to *Ancylocoelus frequens*, but differs by its longer ectoloph relative to transverse dimensions of upper cheek teeth (mesiodistal dimensions of premolars about 77%–82% that of transverse dimension of *Elmerriggsia*, but only 64%–68% in *Ancylocoelus*), base of labial cingulum with a rectangular form (parabolic in *Ancylocoelus*), smoother ectoloph (sharp paracone ridge in *Ancylocoelus*), absence of intermediate lingual cingulum between mesiolingual and distolingual cingulae, mesiolingual cingulum of M1 does not extend to "pseudohypocone" but terminates at mesiolingual corner of protoloph, cristae of ectoloph completely consolidated without tendency to form a split anterior horn of central valley, and lower incisors more gracile than the robust incisors of *Ancylocoelus*.

Larger than *"Henricofilholia" lustrata* and *"H." vucetichia*, with linear dental dimensions about 25% greater than those of these two diminutive leontiniid species from the Gran Barranca (Riberio et al., 2010) referred to *"Henricofilholia."* (Quotes are to suggest that these two species are probably not closely related to "*Parastrapotherium*" *cingulatum* Ameghino, 1894,

which Ameghino ultimately specified as the genotypic species for *Henricofilholia* (Ameghino, 1895). (See Shockey, 2005 for discussion).

Similar in size to *Colpodon propinquus* and *Colpodon antucoensis*, but with less sinuous ectolophs of upper molars and premolars (e.g., paracone ridge is low), has a crest from the protoloph to the mesiolingual cingulum of the upper premolars (generally absent in *Colpodon*), mesiolingual cingulum and distolingual cingulum on nearly the same plane with no connecting intermediate lingual cingulum, and cuspules and cristae of the upper molar and premolar ectolophs well consolidated, resulting in absence of strong undulations, forking, or pitting between internal valley and ectoloph.

DESCRIPTION: *Elmerriggsia* is a much smaller animal than *Leontinia gaudryi*, *Scarrittia canquelensis, Anayatherium fortis*, and *Huilatherium pluriplicatum*. It is also smaller than *Scarrittia barranquensis,* but it is larger than the Gran Barrancan species referred to *Henricofilholia* (*"H." lustrata* and *"H." vucetichia)*. M1 dimensions of *Elmerriggsia* are a little greater than those of *Ancylocoelus frequens* and *A. ekecoa* (see Shockey, 2005: fig. 1, which included P 13386 [now the holotype *Elmerriggsia*] in the graph as an unnamed species [the spelling of *A. "ekekoa"* on the graph is a lapsus calami]). P 13379 is a premaxilla with a fused fragment of the maxilla. It contains teeth we interpret as I2, I3, and C. The placement of the latter tooth just posterior to the premaxilla-maxilla suture leaves no doubt as to its identification as a canine. The most anterior region of the premaxilla was not preserved, so it is impossible to determine whether there had been an I1 in life. The I2 is greatly enlarged compared to the I3 and upper canine. Only the tip of the labial side of the crown of I2 has any enamel. Unlike the I3 and C, the tusk-like I2 has no cingulae. I3 and C are very similar in form, each having an ectoloph that has a simple convex curvature, except for the borders, which are lined on the mesial, basal, and distal sides with a sharp cingulum. The lingual sides of the I3 and C form simple shallow convexities that also are bordered on three sides by a cingulum. Both the I3 and C possess a small parastyle which grades into the mesial cingulum, upon which some occlusal wear has occurred.

Various cheek teeth are preserved in several specimens, of which the most complete is the holotype (fig. 5A), a specimen that Bryan Patterson used as a model for the general dentition of *Leontinia* (Patterson, 1934). The P1 is missing on the holotype, but is preserved on PM14661 (fig. 5C). The P1 (likely dP1, as notoungulates rarely replace the first premolar) is similar to that of *L. gaudryi*, described and figured by Patterson (1934: fig. 10a) with the greatest differences due to the greater wear of the *Elmerriggsia* specimen. Some differences, however, are not attributable to wear or ontogeny. The P1 of *Elmerriggsia* clearly has a weaker mesial cingulum than does *L. gaudryi*, which is manifest by an incomplete connection between the parastyle and protocone and by a shallower mesiolabial cingulum.

Like the P1, all the remaining upper premolars have greater transverse than mesiodistal dimensions, although this transverse elongation is not as great as that of *Ancylocoelus*. At the occlusal level, they appear squared, with subtle undulations of the ectoloph and the distinctive vertical groove of the paracone. P 15060 is an unworn P3 (fig. 5D). It illustrates the basic structure of P2–4 of *Elmerriggsia* and is described and discussed in detail below because it is instructive for comparison to other toxodontians.

Table 3. Measurements (mm) of dentitions of *Elmerriggsia fieldia*, new taxon. Upper table is of the upper dentitions of identified individual specimens, whereas the lower table gives the mean, standard deviations (SD), observed range (OR), and coefficient of variation (CV) of four specimens.

Tooth		P 13386*	P13397	PM 61101
I2	Mesiodistal		28.2	
	Labiolingual		20.1	
I3	Mesiodistal		9.1	
	Labiolingual		7.2	
C	Mesiodistal		10.9	
	Labiolingual		10.4	
P1	Mesiodistal			11.0
	Labiolingual			14.2
P2	Mesiodistal	17.7		17.6
	Labiolingual	21.9		21.5
P3	Mesiodistal	18.4		18.4
	Labiolingual	23.4		23.7
P4	Mesiodistal	20.0		
	Labiolingual	25.7		
M1	Mesiodistal	31.0		
	Labiolingual	30.3		
M2	Mesiodistal	37.6		
	Labiolingual	32.5		

*Holotype

Summary data of lower dentitions (n = 4) of *Elmerriggsia fieldia*, new taxon.

Tooth	Mean	SD	OR	CV
p4 Mesiodistal	19.48	0.340	19.0–19.8	0.017
p4 Labiolingual	15.15	1.162	13.5–16.1	0.077
m1 Mesiodistal	26.60	0.829	25.9–27.8	0.031
m1 Labiolingual	15.20	0.365	14.8–15.6	0.024
m2 Mesiodistal	31.12	1.389	29.2–32.4	0.045
m2 Labiolingual	15.68	1.090	14.5–16.7	0.070

The unworn P3 (P 15060) is composed of an ectoloph connected to the protocone via four crests, the protoloph, metaloph, and the mesiolingual and distolingual cingulae. The ectoloph is rather high, having an enamel surface of 22 mm from the dorsal base of the paracone to its ventral apex, whereas the length of the ectoloph is 18.4 mm (a hypsodonty index of 1.2). The lingual side of the tooth is much shorter, having enamel extending from the tip of the protocone to the base for only 13.3 mm (a hypsodonty index of only 0.72). The ectoloph is not strongly undulating, but has a low paracone ridge, a lower and broader metacone ridge, and a weak distolabial cingulum, but a fairly sharp mesiolabial cingulum. The mesial and distal components of the cingulum unite at the dorsal base of the tooth, whereas the basal part of the cingulum is fairly flat and has a significant horizontal component, in contrast to that of *Ancylocoelus*, in which the basal region of the cingulum has a parabolic form. The protoloph of P 15060 differs from some other premolars of *Elmerriggsia* as it forms a nearly complete ridge from the parastyle to the protocone. The P2–3 protocones of the holotype, however, are not connected to the parastyle at the occlusal level and considerable tooth wear would have to occur before a continuous protoloph would form, as has occurred on P4 of the holotype (compare P4 with P2–3, fig. 5A, or Patterson, 1934: fig. 10c, a line drawing in which these features are unambiguously illustrated). The metaloph, which is clearly defined on P 15060 (fig. 5D), crosses at the most distal region of the ectoloph and arches to the protocone, the apex of which is just anterior to the mesiodistal midline. In the tooth's unworn state, numerous small cuspules and two larger ones form the tips of the crest of the crochet. The crochet arches from the midregion of the metaloph to the midregion of the ectoloph (see fig. 5D). With abrasion, the tips of the cuspules would be worn away to the region where the bases of the cuspules are united as a single mass of dentine (compare the triangular region defined by the crochet, metaloph, and ectoloph of figure 5D with the homologous region of the somewhat worn P3s of fig. 5A and 5C). The mesiolingual cingulum arches from the mesial side of the tooth near the parastyle and obliquely down the lingual face of the protocone to the ventral apex of the protocone. There is a short crest from the junction of the mesiolingual cingulum and the protoloph to the junction of the metaloph and the distolingual cingulum. This distolingual cingulum has a fairly symmetric form relative to that of the mesiolingual cingulum. It, too, arches in the lingual direction away from the protocone then back to form the base of the distal wall of the tooth. There is no trace of an intermediate lingual cingulum between the distal and mesial cingulae on this P3. It is characteristic of upper premolars of *Elmerriggsia* to lack this intermediate lingual cingulum, commonly found in *Martinmiguelia, L. gaudryi*, *Ancylocoelus, Anayatherium* spp., *Scarrittia*. Though it is absent in *Elmerriggsia*, there is a hint of this cingulum on the P4 of the holotype, in the form of a few tiny, barely palpable cuspules. These have collected sediments and been stained in a way that they are readily visible by eye in the photograph (fig. 5A), but would otherwise require magnification to view. (At the scale drawn, the apparent absence of an intermediate lingual cingulum in Patterson, 1934: fig. 10c is correct.) The longitudinal (apex to base) groove of the protocone is distinctive in *Elmerriggsia*, but it also occurs in species that have the intermediate lingual cingulum (e.g., *L. gaudryi, Anayatherium* spp.).

There is no unambiguous association of lower dentitions with those of the uppers; however, the leontiniid mandibles of Pico Truncado are significantly smaller than those of *L. gaudryi* of Cabeza Blanca and La Flecha. They also are of a size such that the holotype can make reasonable occlusal contact with them, and thus are referred to *Elmerriggsia*.

P 13501 (fig. 6) is a nearly complete mandible that preserves at least one example of every tooth. Like those of most leontiniids, the mandibular ramus is deep, but more robust than the relatively more gracile mandible of *Scarrittia* (compare our photo of the jaw of *Elmerriggsia* [fig. 6] with that of *Scarrittia* [Chaffee, 1952: pl. 9.4]). The symphysis is fused and extends to the level of the p4.

The first lower incisor (i1) is the smallest, i2 is a little larger, and i3 is the largest. The i1 is not tusklike, like those of *L. gaudryi*, nor is it especially robust, like those of *Ancylocoelus*. The relatively larger lateral incisors coupled with occlusal wear form a concave anterior bite, allowing for the passage and occlusion of the large, caniniform I2 with i1.

The canine is incisiform and small, about the size of i2. The p1 is also small and single rooted, as are all the teeth anterior to it. The most conspicuous feature of the p1 is the broad longitudinal ridge of the protoconid that forms a blade along nearly half the length of the tooth. The p2–4 are double rooted and have lower crowns than the homologous teeth of *Scarrittia* at a similar wear stage. The p2–p3 have relatively large protoconid ridges and larger "paraconids" than the premolars of *Scarrittia* and *Colpodon*. The metaconid forms the apex of the premolars in lateral view, which have greater wear fore (along the protoconid and "paraconid") and aft (along the short talonid). The p3 has a small entolophid; the entolophid is somewhat larger on p4. All of the premolars possess labial cingulids.

The m1 is so heavily worn on P 13501 that the entolophid fossettid has worn away completely, as have the sulci between the "paraconid" and metaconid and between the entolophid and hypolophid. These features are retained in less worn examples of *Elmerriggsia* teeth (e.g., P 13386), which display the 7/9 morphology typical of lower leontiniid molars, where a right trigonid has the form of the number 7 in occlusal view and the talonid is shaped like the number 9 (the entolophid fossettid representing the center of the circle of the upper part of the 9, and the hypolophid the tail of the 9 [Shockey et al., 2004: fig. 1c]).

PM 413 is a robust calcaneum from Pico Truncado (fig. 7A) that is considerably smaller than that of *Scarrittia* (fig. 7C). It is similar to the Deseadan calcaneum documented by Gaudry (1906), along with an associated astragalus, which he referred to "*Colpodon*" *gaudryi* (= *Leontinia gaudryi*). The calcaneal tuber is so short that the dorsal prominence is located midway on the body. The robust fibular facet dominates the surface of the dorsal prominence, which is orthogonally directed and wedge shaped, with the transverse dimension of the proximal region of facet greater than that of the distal end of the facet. The surface of the fibular facet is convex in the anteroposterior direction, but transversely flat. The ectal facet is more proximally placed than the fibular facet, and is fairly broad, but not as steeply inclined as those of notohippids and toxodontids. The sustentacular facet is smaller in area than either the ectal or fibular facets. The proximodistal dimension of the sustentacular facet is almost twice as great as the transverse. The sustentaculum is short and thick. A

broad tendonal groove for the flexor hallicus longus (or similar flexor) broadly undercuts the posteroplantar aspect of the sustentaculum. The cuboid facet is almost perfectly flat. It is strongly inclined, resulting in a calcaneocuboid articulation at about 45° to the long axis of the calcaneum, much like that of nesodontine toxodontids. An articular ridge runs parallel to the cuboid facet on the medial side of the calcaneum. The proximal side is a distal astragalar facet and the distal side forms a navicular facet, indicating the "reverse alternating tarsus" noted by Cifelli (1993) for various notoungulates and documented below for *Scarrittia* (fig. 7C).

A right astragalus (PM 415: fig. 7B) has the same field number (F 700) as the calcaneum (PM 413), suggesting that they may have been found near one another. These elements articulate well enough with one another to suggest that they are from the same individual. The astragalus has a large body and a very short neck. The trochlea is shallow, both in terms of curvature and depth of the central longitudinal groove. Its convexity is low in lateral view. The lateral trochlear crest is higher than the medial. There is no superior astragalar foramen, but a deep longitudinal groove is present at the proximal extreme of the trochlea, extending to the plantar surface where it contacts a twinned plantar astragalar foramen. The proximomedial extreme (the "dorsomedial tuberocity" noted by Chaffee, 1952, on the astragalus of *Scarrittia*) is not as large as that of *Scarrittia*.

The astragalar neck is very short and has a broad head. There is no ridge between the trochlea and the articular surface for the navicular. The lateral extreme of the head is broken, but remaining portions indicate that the navicular facet extended well beyond the midline of the element. The transverse dimension of the head is half again as long as its greatest dorsoplantar dimension. The breakage of the medial part of the head also removed the distal end of the sustentacular facet, which did not appear to be very long. The remaining part of the sustentacular facet is flat. The ectal facet has but a slight concavity and it extends more distally than the sustentacular facet.

Comments: Patterson (1934) referred to this taxon as *Leontinia* sp. and used the dentitions to exemplify the premolar and molar morphology of *Leontinia*. He indicated that a more detailed study of leontiniids was forthcoming, however, other projects and the inconvenience of mortality prevented that work from being accomplished.

This new taxon, *Elmerriggsia*, is not uncommon among remains from Pico Truncado but we are unaware of its presence in any other Deseadan local faunas. It is significantly smaller than *L. gaudryi*, which is common at Cabeza Blanca (Loomis, 1914) and La Flecha (personal obs., specimens collected by Riggs in the Field Museum). It is similar in size to *Ancylocoelus frequens* (specimens of which were collected by the Riggs party from La Flecha, but not at Pico Truncado or Cabeza Blanca), but is easily differentiated from *A. frequens* (see differential diagnosis).

Leontiniid Postcranial Skeleton

Aside from the monographic work describing complete skeletons of *Scarrittia* (Chaffee, 1952), little has been reported regarding the postcrania of leontiniids. The sum of knowledge

of postcrania of leontiniids other than *Scarrittia* is minimal and includes elements referred to *Colpodon* (astragalus noted, but not figured by Ameghino, 1902), *Leontinia gaudryi* (proximal tarsus figured by Gaudry, 1906: fig. 46; an atlas, axis, humerus, and ulna described and figured by Loomis, 1914), and *Taubatherium paulacoutoi* (proximal ulna and radius and calcaneum described and figured as "*Leontinia* sp." by Paula Couto, 1983). Here we briefly summarize the known postcranials of leontiniids and add a few new observations. Our phylogenetic analysis of leontiniids includes 43 postcranial characters, a substantially greater number than included in prior analyses of this or related notoungulate groups.

Axial Skeleton: The most conspicuous feature of the axial skeleton of *Scarrittia canquelensis* was its elongated neck (Chaffee, 1952). Chaffee noted that this elongation was greater than that of the neck of the other notoungulates (the toxodontids *Nesodon* and *Adinotherium* and the homalodotheriid *Homalodotherium*) to which he compared it. He did not compare it to the poorly known neck of *Leontinia*, but that of *Leontinia* may be shorter, as evidenced by the greater relative total length of the axis (centrum + odontoid process) compared to the width of the axis at the condyles. This ratio is 1.60 in *Scarrittia* (AMNH 29584: odontoid + centrum = 163 mm/condyle width = 102 mm) but only 1.35 in *Leontinia* (Loomis, 1914). It also is relatively short in outgroups. Thus, until the cervical regions of other leontiniids become better known, the elongated neck of *Scarrittia* is best regarded as autapomorphic.

Scapula: The scapula of leontiniids has been documented only for *Scarrittia* (Chaffee, 1952; see also fig. 10). We note a scapula in the FMNH Riggs collection that is referable to *Leontinia gaudryi* of Cabeza Blanca (P 12684). The supraspinatus fossa is badly damaged, but the border at its medial extreme suggests that it was much smaller than the infraspinatus fossa. The high scapular spine lies at an angle such that it leans over the supraspinatus fossa and away from the relatively large infraspinatus fossa. Although the acromion sits high on the spine, it is recessed away from the region above the glenoid fossa. There is no evidence of a metacromion. The glenoid has a teardrop form in which the apex lies opposite the coracoid region. The coracoid region is blunt and rounded, lacking a distinct coracoid process. Compared to the scapula of *Scarrittia*, that of *Leontinia* differs by way of a less developed coracoid process and apparent absence of a well-developed metacromion. The available specimens also suggest that the overall outline is less rounded than that of *Scarrittia*, and that there are unequal relative sizes of the supraspinatus and infraspinatus fossae, with *Leontinia* appearing to have a smaller supraspinatus fossa.

Humerus: The humerus is known for both *Scarrittia* (Chaffee, 1952) and *Leontinia gaudryi* (Loomis, 1914; and AMNH 32774). They are similar in these two taxa in both having a reduced medial epicondylar processes, no entepicondylar foramen, weakly developed supinator crest, and similar antebrachial articular morphology wherein the transversely concave trochlea grades into the convex capitulum.

Forearm: Significant components of the antebrachium of leontiniids are known for *Scarrittia, Leontinia*, and *Taubatherium* (Loomis, 1914: fig. 77; Chaffee, 1952; and Paula Couto, 1983: figs. 9, 14a, b). All three have olecranon processes that are directed in the ventral direction, as occurs in most "advanced Toxodontia" (e.g., *Nesodon* and *Adinotherium* [Scott, 1914], *Rhynchippus equinus* [FMNH 13410]), and is typical for ungulates having an erect stance (Van

Valkenburgh, 1987; Shockey and Flynn, 2007), but differs in the notohippid *Eurygenium* (Shockey, 1997) and from many typothere notoungulates (e.g., *Protypotherim* [Sinclair, 1909] *Trachytherus* [Shockey et al., 2007]), which have olecranon processes that are somewhat dorsally directed (indicative of a crouching stance [O'Leary and Rose, 1995; Van Valkenburgh, 1987; Shockey and Flynn, 2007].

Manus: *Scarrittia* is the only leontiniid in which the hand is satisfactorily known (Chaffee, 1952). It is mesaxonic and pentadactyl, but digits I and V are much reduced compared to II–IV. Metacarpals II–IV are subequal in length and are half again as long as the metatarsals. Two carpals of a leontiniid were collected at Pico Truncado on the Marshall Field Expedition, a right lunar (PM 411) and a right unciform (PM 412). Aside from one significant detail (below), they are of a similar size and morphology to the homologous elements of *Scarrittia*, so there is no real doubt as to their identification as a leontiniid, but it is uncertain to which of the leontiniids of Pico Truncado it pertains (*Elmerriggsia* or *Leontinia*). The anatomical fit is imperfect enough to suggest that they are from two individuals. The unciform is instructive, because the distal facet is a simple concavity that has subequal transverse and dorsopalmar dimensions. Unlike the unciform of *Scarrittia*, which has a small Mt V facet on the same plane as the Mt IV facet, there is no evidence of a facet for Mt V. This suggests that Mt V is more reduced (perhaps absent) in the Pico Truncado taxon than in *Scarrittia*.

Femur: Regarding the femur of *Scarrittia*, Chaffee (1952) documented the prominent head, the distinct neck and greater trochanter, and the proximally placed third trochanter, but said nothing of the distal region of the element, perhaps owing to the distortions in all the available material.

A left distal femur and proximal tibia (P 13632, fig. 8A) in the FMNH collection is referred to *Leontinia gaudryi*. This specimen is distinctive in regard to the asymmetry of its patellar groove; the medial trochlear ridge is longer than the lateral, but it does not appear to have been significantly higher (some damage makes it impossible to assert this with great confidence). Also, proximal to the patellar groove, the lateral region of the cranial face of the femoral shaft forms a longitudinal suprapatellar keel that is much higher than the rest of the cranial face of the distal region the shaft. A cross section at this region would have the form of a blunt comma, in which the concave side of the comma would represent the cranial face of the shaft and the tail of the comma the medial ridge. How far this extends up the shaft cannot be determined from available material.

A distal femur from the Salla, Bolivia, of late Oligocene age (UF 225743; fig. 8B) is referred to *Anayatherium*, cf. *A. fortis*. Like the femur of *Leontinia*, it has a suprapatellar keel; however, its distal component is more pronounced and it grades into an enlarged and elongated medial trochlear ridge of the knee.

Crus: Chaffee (1952) suspected that the proximal tibia and fibula of *Scarrittia* were fused in life, but he was unable to assert this definitively, due to damage of material he studied. Proximal tibiofibular fusion is unambiguously shown in the proximal tibia-fibula (P 13632) of the leontiniid crus from Pico Truncado. However, it is not certain if that specimen pertains to *Elmerriggsia* or *Leontinia*.

Pes: *Scarrittia* is the only leontiniid for which the foot is completely known. Chaffee reconstructed it as being pentadactyl, although functionally tridactyl. It is interpreted as having been semidigitigrade, with the long plantar processes suggestive of having supported a significant footpad that resulted in the calcaneum being raised somewhat from the ground by supportive tissue (Chaffee, 1952). Proximal tarsals are documented for some other leontiniids, including *Leontinia gaudryi* (Gaudry, 1906), *Scarrittia*, *Taubatherium* (Paula Couto, 1983), and now *Elmerriggsia* (above). Several distinctive traits are common to all of these leontiniids, including some characteristics more inclusively shared with notohippids and toxodontids. These "advanced toxodont" traits include calcaneonavicular articulation ("reverse alternating tarsus" sensu Cifelli, 1993) and a strongly developed fibular facet that is dorsoventrally (not obliquely) directed. Peculiar to the leontiniids (*Scarrittia*, *Leontinia, Elmerriggsia*, and *Taubatherium*) is the distinctive form of the fibular facet, which has the greater transverse dimension at the proximal border compared to the distal (fig. 4).

Character Analysis

We developed the following character analysis based upon our original studies of specimens, complemented by published descriptions and illustrations. Appendix 2 lists the published sources and the instructive specimens we examined.

Some data obtained in this study also augment and correct observations from previous studies of leontiniids. For example, Shockey (2005) indicated that the presence or absence of I3–P1 of the holotype of *Anayatherium fortis* could not be ascertained. However, AMNH preparator Edward Pedersen expertly removed matrix that had obscured the alveoli of the holotype, so that we can now objectively assert that *A. fortis* had a complete (3-1-4-3) upper dental series, including I3–P1 (fig. 9A). Also, our conclusions regarding the state of the molar mesiolingual cingulae of *Taubatherium* differs from that of Villarroel and Colwell Danis (1997) who reported it as absent; the molars of *T. paulacoutoi* do indeed have a mesiolingual cingulum (Soria and Alvarenga, 1989: fig. 3).

Whenever possible, we modified our descriptions and scorings so that they would be compatible or interchangeable with characters previously defined and used in the literature (e.g., Cifelli, 1993; Villarroel and Colwel Danis, 1997). This was done in an effort to approach a convention or standard so that analyses may be more universally applicable and comparable. In some cases we needed to modify some character definitions or scoring to better capture the morphological states in the taxa used in this study. Where we used or modified character states from the literature, we cite the source and give the character number (#) used in the original study. The work of Cifelli (1993) contained several notoungulate analyses, however, our discussion here is limited to his analysis of the "Advanced Toxodont Families" (Cifelli, 1993: appendix 4).

The characters selected and defined in this study were those that were most relevant for understanding relationships among the Leontiniidae and across the Toxodontia. Other notoungulate taxa were included as near outgroups; however, we defer any broader phylogenetic conclusions regarding the relationships among those outgroup taxa for other works we currently have in progress.

Morphological descriptors that include a taxon name were avoided. Specifically, we do not use "leontiniid basin," which was defined by Colwell (1965) to note the region demarcated by the mesiolingual cingulum of the upper premolars. Although this convention has been followed by Villarroel and Colwell Danis (1997) and Shockey (2005), we regard it as undesirable since it implies a predetermined taxonomically diagnostic value (putting the cart before the horse) which, in this case, is inappropriate, since the complex of protoloph and mesiolingual cingulum manifests itself such that "leontiniid basins" also occur in some notohippids (e.g., *Rhynchippus equinus* [Ameghino, 1897] and *Pascualihippus* [Shockey, 1997]). Instead, we simply note the presence/absence of the mesiolingual cingulum (character #21), and code the various forms of the premolar protoloph that affect the appearance of the mesiolingual cingulum (chars. #23, #24, and #25).

For the purposes of exploring character states of basal notoungulates and for future higher-level phylogenetic studies, we did not exclude characters found to be universal among the notoungulates. Their ubiquity among notoungulates rendered them useless for the purposes of discovering phylogenetic relationships within notoungulates; however, such characters are not uninteresting, since they may be derived when compared to non-notoungulate outgroups. Fusion of the mandibular symphysis and absence of centrale, for example, were ubiquitous among our survey of notoungulates, but differ in outgroups. The relevance of these characters is noted in the discussion section.

1. Cheekteeth orientation: (0) strong anterior convergence of cheek teeth, resulting in the distance between left and right P1s being less than half that of the distance between left and right M2s, such that the upper dental arcade will appear V-shaped (fig. 9A); (1) no substantial anterior convergence of cheek teeth (the distance between left and right P1 is greater than half the distance between the M2s) with the anterior dental arcade U-shaped; (2) anterior dental arcade transverse and [-shaped. Modified from Cifelli (1993: #5 of the "advanced toxodont families" analysis) and Shockey (1997: # 6).

Cifelli's (1993) version of this character was defined as "(f)orm of anterior dental arcade" as "V-shaped" or "U-shaped." With the exception of *Colpodon*, Cifelli (1993) scored all leontiniids as having V-shaped anterior dental arcades, whereas those of notohippids where characterized as "U-shaped." Inexplicably, Cifelli (1993) scored all the toxodontids in his analysis as having V-shaped arcades, when in fact the anterior dental arcade of toxodontids is very blunt (not coming to a point), having a transverse dental arcade. Indeed, toxodont dental arcades deviate further from a V-shaped muzzle even more than do notohippids, which Cifelli (1993) characterized as U-shaped. The present character analysis thus includes three general forms of the anterior dental arcade: V-, U-, and [- shaped, the latter a shorthand designation of the transverse dental arcade of toxodontids and the notohippids *Eomorphippus* and *Pascualihippus* (in this convention the anterior muzzle is directed to the left in the [-shaped snout, whereas it is directed downward in the U-shape and V-shape). The U-shaped dental arcade is presumed to be the plesiomorphic form within Notoungulata, as it is common across most clades, and non-notoungulate ungulates.

2. Upper dental formula: (0) complete upper dentition, (1) C absent; (2) more than one upper

tooth (the canine and another tooth). Modified from Villarroel and Colwell Danis (1997: #1).

3. Relative canine size: (0) caliber and height of canine greater than any of the incisors; (1) canine subequal in size to incisors, but none of the incisors are greatly enlarged; (2) one of the incisors is caniniform and larger than any canine.

4. I1 form: (0) incisiform (labiolingual compression, with transversely flat occlusal surface); (1) caniniform (ovoid or round in cross section with pointed cusp); (2) gliriform, much larger (broader and taller) than lateral incisors (if present).

5. I1 enlarged caniniform: (0) absent; (1) present.

6. I2 enlarged caniniform: (0) absent; (1) present.

7. Labial cingulum of upper incisors presence/absence: (0) present in all incisors except any that are hypertrophied; (1) absent.

Bond and López (1995) recognized the labial cingulum of the brachydont incisors as a diagnostic character for leontiniids. They included *Colpodon* in the Leontiniidae, based on the finding of incisive cingulae in a specimen they studied. The specimens we observed, however, lacked a cingulum, so *Colpodon* is scored as variable for this character (0/1).

8. Incisor root form: (0) incisors with determinate growth, roots form after crown formation; (1) incisors hypselodont (never form roots).

9. Diastema in anterior upper dentition: (0) absent, no significant gaps between anterior upper teeth; (1) present, large gap between anterior teeth and cheek teeth.

We ignored numerous and variable small gaps among teeth in scoring for the presence of diastemata. We regard a diastema as present only when a gap is larger than expected for a single tooth (typical of the region) to occupy.

10. Upper premolar root form: (0) upper premolars with determinate growth, roots form after crown formation; (1) premolars hypselodont, roots do not form at least one premolar is hypselodont.

11. Upper molar root form: (0) all upper molars with determinate growth, roots form after crown formation; (1) molars hypselodont, roots do not form.

12. Relative height of M1: (0) brachydont (hypsodonty index [HI] of M1 < 1); (1) mesodont (HI of M1 ≈ 1); (2) M1 hypsodont (HI > 1); (3) M1 euhypsodont (HI > 2) (adapted from Shockey, 1997: #11).

13. Cementum: (0) absent; (1) variably present or present in small amounts on one or more tooth; (2) thick coating of cementum is invariably present (adapted from Cifelli, 1993: #12).

As in other ungulates (e.g., horses and cows) the evolution of cementum-covered crowns appears to have occurred independently among several groups of notoungulates.

14. P1 orientation: (0) ectoloph in same plane as that of the other upper premolars; (1) ectoloph obliquely oriented, parastyle distinctly medial to the paracone.

15. Parastyle cingulum of P1–3 form: (0) may be separated from paracone ridge by a longitudinal valley, but does not form a sharp, distinctive mesiolabial "cingulum" that extends from the crown to the base of the tooth; (1) parastyle forms a sharp, distinctive mesiolabial "cingulum" that extends from the crown to the base of the tooth.

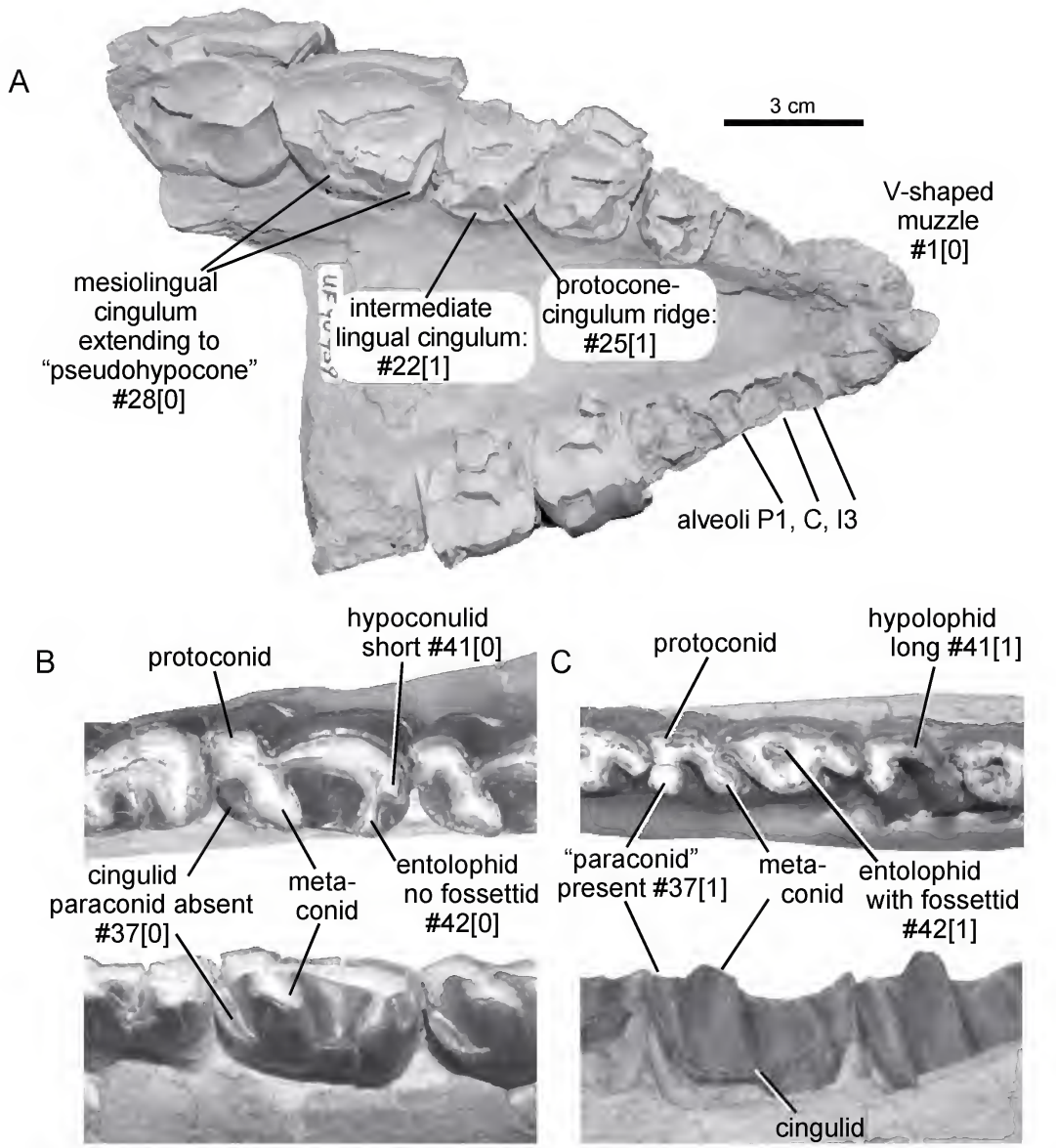


FIGURE 9. Selected dental characters of **A,** *Anayatherium fortis*, cast of holotype, alveoli of I3–P1 are exposed to show that *A. fortis* had a complete dental formula; **B,** m2 of *Thomashuxleya externa* (AMNH 28697) in occlusal (upper) and oblique (lower) views; and **C,** left m2 of *Scarrittia canquelensis* (AMNH 29592) in occlusal (upper) and lateral (lower) views. B and C illustrate the hypothetical evolution of the "paraconid" from the mesiolingual cingulid.

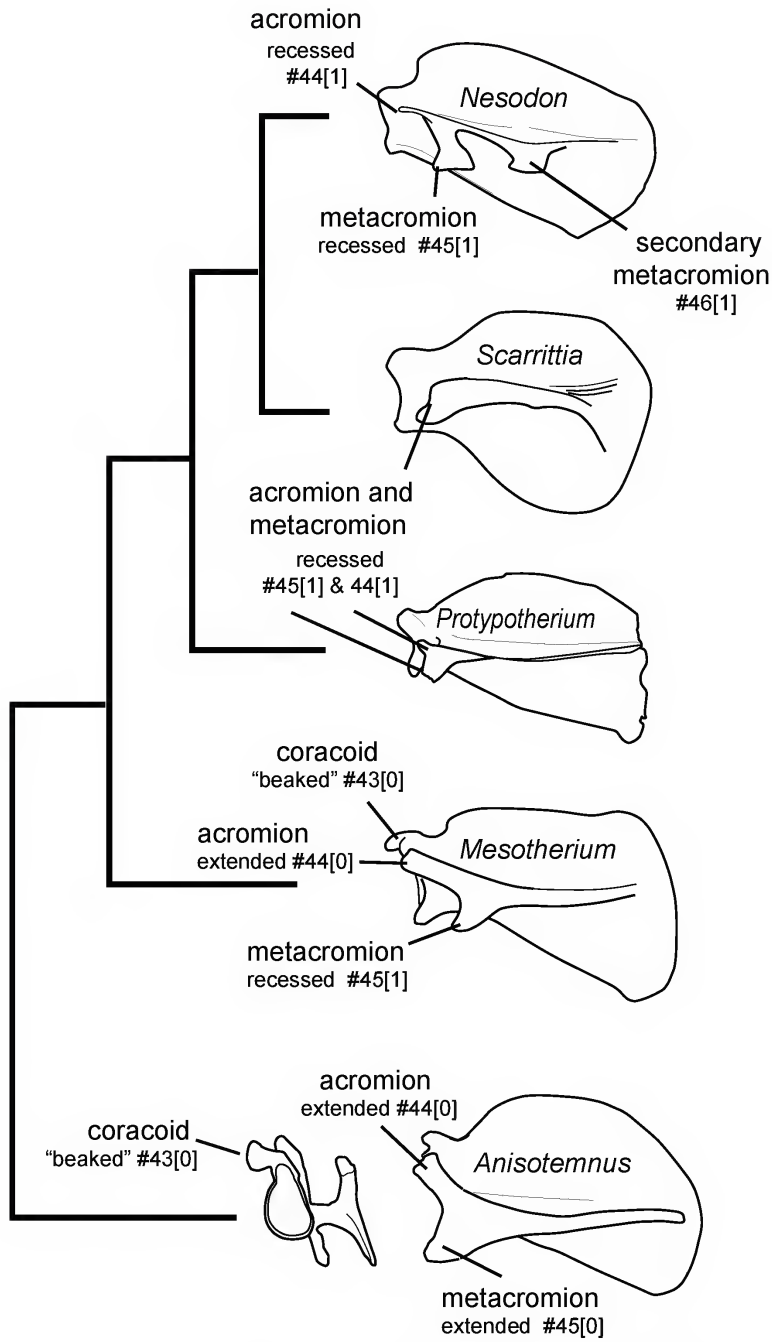


FIGURE 10. Hypothetical scapular transition series in Notoungulata. Not drawn to scale.

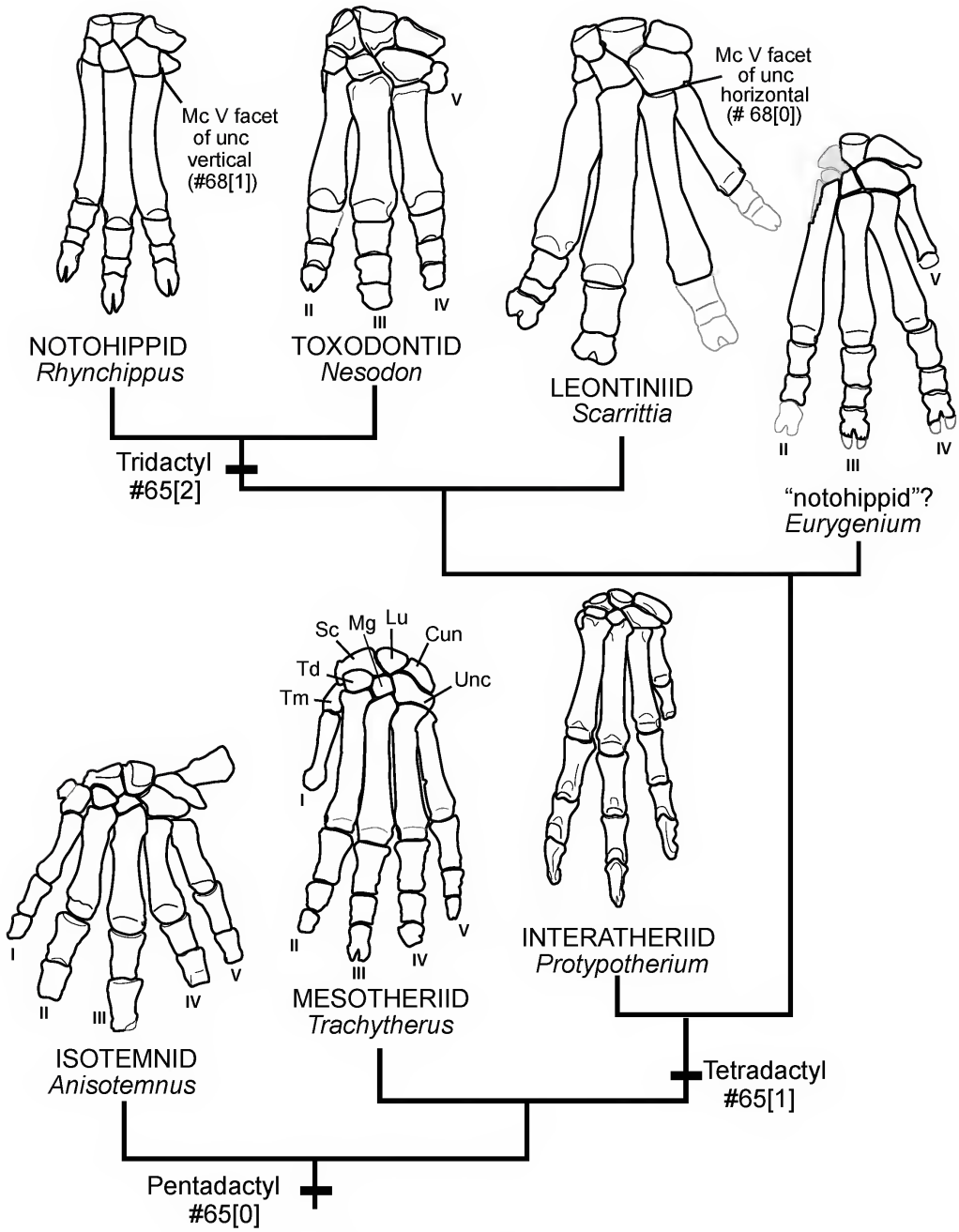


FIGURE 11. Hypothetical manual transition series in Notoungulata. All hands shown as left. Not drawn to scale. Abbreviations: Cun, cuneiform; Lu, lunate; Mg, magnum; Sc, scaphoid; Td, trapezoid; Tm, trapezium. Roman numerals indicate digit number.

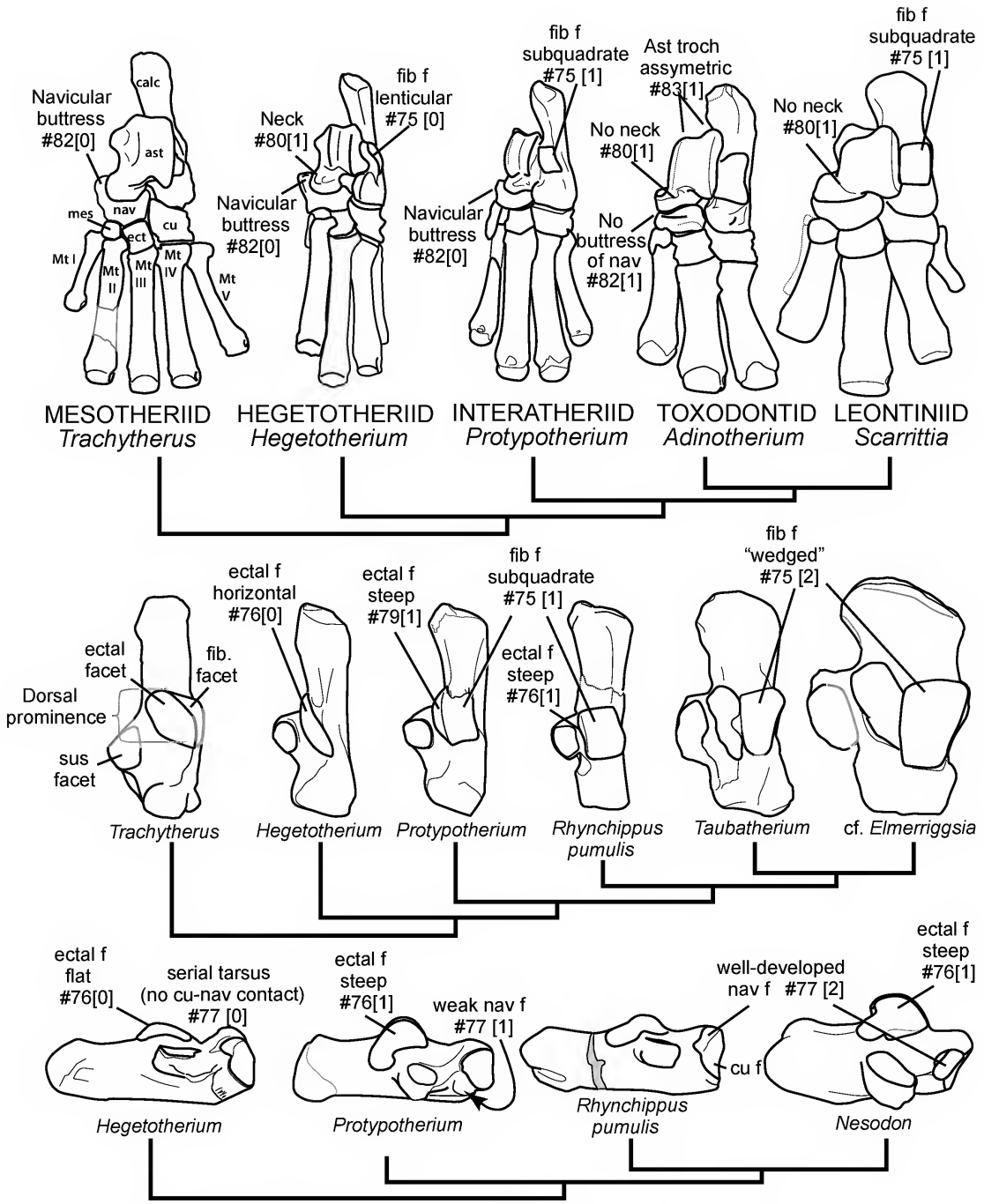


FIGURE 12. Hypothetical pedal transition series in Notoungulata showing left pes in dorsal view (upper row), left calcaneum in dorsal view (middle row), and left calcaneum in medial view (lower row). Illustrations are not to scale. Abbreviations are as follows: ast, astragalus; calc, calcaneum; cu, cuboid; ect, ectocuneiform; f, facet; fib, fibula; Mt, metatarsal; nav, navicular; sus, sustentacular; troch, trochlea.

16. Labial cingulum of P1–3 presence/absence: (0) present, lies at the base of the tooth between the paracone ridge and the metacone ridge; (1) absent.

17. Distolabial cingulum ("metastyle") of P1–3 presence/absence: (0) absent; (1) present, distinctive longitudinal cingulum forms a sharp distal border of the ectoloph.

18. Cristae of upper premolar ectolophs: (0) separate cristae from ectoloph persist with modest wear, manifested by small loops in the labial side of the major fossette or enamel-lined pits between the fossette and ectoloph; (1) one or two cristae persist with moderate wear giving the central valley (or fossette) a branching appearance; (2) separation between cristae very shallow and quickly obscured by wear.

19. P2–4 protoloph: (0) robust, base inclined and extends to lingual extreme of tooth; (1) relatively small and recessed from lingual extreme, not inclined toward mesiolingual cingulum.

20. Upper premolar mesiolingual cingulae: (0) present; (1) absent. (Shockey, 1997: #16)

21. Upper premolar distolingual cingulum position: (0) distolingual cingulum far removed from the occlusal surface in little worn teeth, may be a little closer to crown than the mesiolingual cingulum; (1) distolingual cingulum close to crown (closer to crown than mesiolingual cingulum, if present) with tendency to come into wear early and produce mesiodistal bulge that extends more lingual than the protoloph; (2) tendency for distolingual cingulum to form distinctive "cup" (sensu Patterson, 1934.)

22. Upper premolar intermediate lingual cingulum extent: (0) no lingual cingulum, or if mesiolingual and distolingual cingulae are present they are not united by lingual (intermediate) cingulum; (1) mesiolingual and distolingual cingulae are united by intermediate lingual cingulum.

23. Upper premolar protocone lingual face groove: (0) absent, without vertical groove; (1) present, with vertical groove on lingual face (fig. 5; Patterson, 1934).

24. Mesiolingual face of upper premolar protoloph ridge: (0) absent, without ridge to mesiolingual cingulum; (1) present, with ridge to mesiolingual cingulum (separates the "leontiniid basin" in species having the ridge as well as mesio- and intermediate lingual cingulae [e.g., *Leontinia gaudryi* and *Anayatherium fortis:* fig. 9A]).

25. Labial cingulum of M1 presence/absence: (0) present; (1) absent.

26. Cristae of upper molar ectolophs, persistence with wear: (0) separate cristae from ectoloph persist with modest wear, manifested by variable numbers of small loops in the labial side of the major fossette or enamel-lined pits between the fossette and ectoloph; (1) one or two cristae persist with moderate wear giving the central valley (or fossette) a branching appearance; (2) separation between cristae very shallow and are quickly obscured by wear.

27. Dominant upper molar crista: (0) no single crista dominates; (1) first crista dominates, forming branch of anterior region of central valley.

28. M1 mesiolingual cingulae: (0) present, extends to "pseudohypocone"; (1) present, extends only to protoloph; (2) absent.

29. Posterior cingulum of upper molar form: (0) does not form distinct oval fossette with wear; (1) forms distinct oval fossette with wear.

30. Lower incisor orientation: (0) long axis of lower incisors directed relatively vertically, at an angle greater than 40° to long axis of mandible; (1) incisors procumbent, long axis of incisors more in line with long axis of mandible (angle to mandibular ramus <40°).

31. Third lower incisor (i3) size: (0) not enlarged relative to other incisors; (1) larger than other lower incisors.

32. Third lower incisor (i3) form: (0) incisiform; (1) caniniform or tusklike; (2) peglike, very small or absent.

In leontiniids and toxodontids, the i3 is larger than either of the mesial incisors and the canine. The cross section of the hypertrophied i3 is generally triangular in both leontiniids and toxodontids, but that of toxodontids tends to appear more spatulate ("incisiform"; Scott, 1912a) than the i3 of leontiniids.

33. Lower incisor labial cingulum presence/absence: (0) present; (1) absent.

34. Metaflexid of lower premolars shape: (0) simple without branching; (1) with bifurcations (adapted from Villarroel and Colwell Danis, 1997: #18).

35. Lingual cingulid of lower premolars: (0) distinct and continuous along the length of the tooth; (1) not distinct along metaconid, but appears anterior to metaconid and between metaconid and entoconid (or entolophid); (2) entirely absent (except for what may be manifest as a "paraconid" [see Discussion and figs. 9B, C]).

36. Labial cingulid of p2–p4: (0) present on p2–p4; (1) present on p2, but absent on p4; (2) absent on p2–p4. Modified from Villarroel and Colwell Danis (1997: #19) to include absence of premolar labial cingulid.

37. Lower molar "pseudoparaconid" presence/absence: (0) absent or minute; (1) presence of a substantial "pseudoparaconid" in a position similar to that of a paraconid, although it may be derived from the mesiolingual cingulum, rather than representing a true trigonid paraconid.

Cifelli (1993) noted the absence of the paraconid in early (Paleocene-Eocene) notoungulates and suggested that the lack (loss) of a paraconid is a synapomorphy for Notoungulata. Later notoungulates (e.g., leontiniids and many others) have a lophid that extends to the mesiolingual corner of the tooth suggestive of a paraconid-protoconid connection. Our observations of progressive occlusal wear in *Thomashuxleya*, however, suggest that this lophid originates from the mesial cingulid, which grades into the protoconid of *Thomashuxleya* and extends to the labial side and comes into occlusion as a functional lophid once occlusal wear has occurred (fig. 9B, C).

38. Lower molar metaconid morphology: (0) forms a simple, oblique crest; (1) possesses an accessory cusp.

Cifelli (1993) considered the presence of this accessory cusp a possible synapomorphy for the Isotemnidae, but noted its variable presence in isotemnids. We failed to find this cusp in our samples of *Thomashuxleya externa*.

39. Labial cingulid of m1 presence/absence: (0) present; (1) absent.

40. Labial cingulid of m2 presence/absence: (0) present; (1) absent.

41. Hypoconulid of m1–2 length: (0) short, extends little beyond the entolophid; (1) elongated, entolophid projects from near midpoint of talonid crest.

42. Molar entolophid fossettid presence/absence: (0) absent; (1) present. (Shockey, 1997: #21).

The entolophid fossettid develops between two transverse lophids that connect to the hypolophid (Loomis, 1914: fig. 52). Loomis (1914) noted these lophids and named the anterior of the two the "septum" and the posterior the "pillar." These unite early in development to form the "entolophid," but a persistent fossettid forms in notohippids (excepting *Eurygenium* and *Morphippus*), basal toxodontids (e.g., *Proadinotherium*, *Adinotherium*, and *Nesodon*), and all known leontiniids. This entolophid fossettid is also known as the "bay 3" fossettid (or "pit 3") (Loomis, 1914) or the "posterior fossettid" (e.g., Soria and Alvarenga, 1989: fig. 1).

We avoid terms that designate relative position (e.g., number or "posterior") since the absence of the related feature may be disorienting (e.g., a "second fossettid" appears absurd if there is no first, as does a fossettid posterior to the "posterior" fossettid). For example, the entolophid fossettid has been called the "posterior fossettid," but a more posterior fossettid frequently forms via the uniting of the hypoconulid with the entolophid (e.g., *Coresodon*, [Loomis, 1914] as well as *Pascualihippus* and *Rhynchippus brasiliensis* [Shockey, 1997: fig. 2]).

43. Coracoid process shape: (0) distinctive, with recurved "beak"; (1) process present, but lacking a "beak"; (2) process indistinct or absent, scapular tuber small. (See fig. 10 regarding this and chars. 44–46.)

44. Acromion border extent: (0) extends distally to near the level of the glenohumeral joint or beyond; (1) limited to the region of the scapular body or scapular neck adjacent to the scapular body, but does not extend toward the region over the glenohumeral joint. Adapted from Meng et al. (2003).

Meng et al. (2003) regarded the condition of an "acromial plate" that overhangs the glenohumeral joint as being the primitive condition for eutherians. The acromial plate forms a fairly symmetric shield that suggests the contour of the proximal humerus. We regard the medial process of the shield as the acromion and the lateral one as the metacromion. (See #45.)

45. Metacromion extent: (0) extends distally to near the level of glenohumeral joint or beyond; (1) limited to the area above the region of the scapular body or the region of the scapular neck adjacent to the scapular body, but does not extend toward the region over the glenohumeral joint.

The spine of the scapulae of the isotemnids *Thomashuxleya* and *Anisotemnus* has paired acromial and metacromial processes that overlie the glenohumeral joint and appears to represent the plesiomorphic eutherian condition (Meng et al., 2003). The acromion and metacromion are located more proximally in most other notoungulates.

46. Secondary metacromion presence/absence: (0) absent; (1) present. The scapulae of the basal toxodontids ("nesodontine" toxodontids) *Nesodon* and *Adinotherium* have two metacromia (Scott, 1912a).

47. Greater tubercle height: (0) lower than the head of the humerus; (1) even with or higher than the head (modified from Rose and Lucas, 2000; and Meng et al., 2003).

48. Bicipital groove closure: (0) well enclosed by greater and lesser tubercles; (1) open, relatively wide space between greater and lesser tubercles.

49. Deltoid crest shape/position: (0) distinctive, extending to more than 2/3 the length of the humeral shaft; (1) distinctive, proximally placed; (2) no well defined crest or tuberocity for the deltoid muscles.

50. Pectoral crest shape/position: (0) distinctive, extending to more than 2/3 the length of the humeral shaft; (1) distinctive, proximally placed; (2) no well-defined crest or tuberocity for the deltoid muscles.

51. Tuberosity for m. teres major presence/absence: (0) present; (1) absent.

52. Supinator crest: (0) present, well developed, broad and bladelike; (1) inconspicuous (grades into shaft) or absent.

53. Entepicondylar process, medial extent: (0) extends medially with a dimension more than half that of the trochlear width; (1) medial extension short (dimension <40% that of the trochlea).

54. Entepicondylar foramen presence/absence: (0) present; (1) absent.

The presence of the entepicondylar foramen is generally regarded as the plesiomorphic condition for mammals (Landry, 1958). It is commonly absent (presumably lost) in terrestrial cursors, such as ungulates and canids. Its near ubiquity in notoungulates (present in isotemnids, and mesotheriids, hegetotheriids, interathertheriids), and presence in many eutherian outgroups, suggests that it, too, is plesiomorphic for Notoungulata. As far as known, it is absent only in the Toxodontia families Homalodotheriidae, Leontiniidae, Notohippidae, and Toxodontidae.-

55. Medial trochlear flange size: (0) large (Shockey and Flynn, 2007: fig. 2a); (1) small. (See Andersson, 2004, regarding function in felids.)

56. Brachial index (BI): (0) length of radius subequal to that of humerus (90 < BI < 100); (1) radius shorter than humerus (BI < 90); (2) radius longer than humerus (BI > 110).

57. Olecranon shape in lateral view: (0) major axis of olecranon the same as that of the ulnar shaft; (1) major axis of olecranon with upward curve (crouching stance morphology); (2) major axis of olecranon with downward curve (erect stance morphology).

Upward olecranon curvature is found in many extant climbing mammals (e.g., the binturong, *Arctictis* [see O'Leary and Rose, 1995: fig. 7], whereas downward curvature is associated with the erect stance of cursorial mammals (e.g., canids, *Lama*). This character varies among notoungulates, even among the few known Eocene forms (downward curvature in *Thomashuxleya*, upward curvature in *Anisotemnus* and *Maxschlosseria*; Shockey and Flynn, 2007).

58. Olecranon shape in dorsal (anterior) view: (0) major axis of olecranon in the same orientation as that of the ulnar shaft, (1) major axis of olecranon with distinct medial curvature (e.g., *Trachytherus*; Shockey et al., 2007).

59. Outline of proximal radial in proximal view: (0) oval; (1) subrectangular. Modified from Meng et al. (2003: #186).

The radial head of the arctocyonid *Chriacus* may represent a model of the plesiomorphic mammalian radial head (see Gebo and Rose, 1993; O'Leary and Rose, 1995). The radial head

of *Chriacus* is oval and has a simple depression for the articulation with the humeral capitulum. The convex and ovoid ulnar facet of the proximal radius facilitates rotation of the radius, whereas such is restricted by the derived flat and subrectangular articulation (char. state 1). The derived form is exemplified by *Phenacodus*, in which the radial head has a transverse dimension more than 1.5 times that of the dorsoventral dimension. The fossa of the radial head of *Phenacodus* is undulating, rather than a simple concavity. (Compare drawings of the radial heads of *Chriacus* and *Phenacodus* in O'Leary and Rose, 1995: fig. 9).

60. Radial head fossa: (0) presence of simple fossa in proximal view; (1) depression of head is undulating. (See note above, #57.)

61. Capitular eminence (central process) of radial head presence/absence: (0) absent, the radial head is smooth or undulating, without distinctive capitular eminence; (1) present, with distinctive (sharp) capitular eminence of the proximal end on the dorsal side (pronated) of the radius.

A distinctive central process on (the "capitular eminence" of some workers (e.g., Gebo and Rose, 1993; Rose and Lucas, 2000) is generally regarded as being an indication of terrestrial locomotion and its absence an indication of climbing ability (Szalay and Sargis, 2001). However, Gebo and Rose (1993) noted that it is present in several extant scansorial and even arboreal mammals, thus discounting the notion that a capitular eminence inhibits rotary movements too seriously to permit climbing. It is more commonly present in terrestrial taxa (e.g., lagomorphs, *Phenacodus*, and *Hyopsodus* [Meng et al., 2003]).

62. Radial sesamoid presence/absence: (0) absent; (1) present.

The presence of the facet on the radius for the radial sesamoid may be used to score its presence/absence, thus this character (#60) may also be stated as the presence of a facet for radial sesamoid on the proximolateral surface of the radius in prone position: (0) absent or (1) present.

"Elbow" sesamoids are known to articulate with the dorsolateral surface of the radial head in several notoungulates, including the nesodontine toxodontid *Nesodon* (Scott, 1912a) and mesotheriid notoungulates, *Trachytherus* and *Plesiotypotherium* (Shockey et al., 2007). Scott (1930) deduced its presence also in *Homalodotherium* via the presence of the extra facet of the proximal radius, which was in the homologous position as that of *Nesodon*. This trait also is known in the pocket gopher *Geomys* (Shockey et al., 2007) and various didelphid and caenolestid marsupials (Szalay and Sargis, 2001, text and fig. 10b, c, f, g). The radial sesamoid (when present) in notoungulates differs from those of marsupials by being a more robust element that correlates with a large dorsolateral facet of the proximal radius, but without any evidence of contact with the humerus. Despite the relatively large size of the notoungulate elbow sesamoid, it may be easily separated from the joint postmortem or missed by collectors. Thus, its presence is most easily deduced by the sesamoid facet of the dorsolateral surface of the proximal radius.

63. Distal radius dorsal outline shape: (0) dorsal outline convex with no styloid process; (1) outline oblique, with no distinct styloid process; (2) outline with distinctive styloid process with facet for scaphoid and lunar on the ulnar side of the process.

A distinctive radial styloid process is absent in a variety of notoungulates, including isotemnids (*Thomashuxleya*, *Anisotemnus*), mesotheriids (*Trachytherus*, *Mesotherium*). Notohippids

(e.g., *Rhynchippus* and *Argyrohippus*) have an oblique border of the distal radius, whereas toxodontids (e.g., *Nesodon*, *Adinotherium*) have a distinctive styloid process.

64: Distal ulna articulation with pisiform presence/absence: (0) present; (1) absent.

Chaffee (1952) noted the absence of ulnar-pisiform contact in *Scarrittia* and *Homalodotherium*, mentioning it as possible evidence of a close phylogenetic relationship between the two taxa.

65. Manus, digit number: (0) pentadactyl; (1) tetradactyl; (2) tridactyl (fig. 11).

66. Relative metacarpal/metatarsal lengths on digit III (Mc III/Mt III): (0) metacarpals subequal in length to metatarsals, with the Mc III-to-Mt III ratio not exceeding 1.5; (1) metacarpals relatively elongate compared to metatarsals, with Mc III/Mt III greater than 1.5.

Whereas small typothere notoungulates (e.g., the Santacrucian interatheriids and hegetotheriids) have longer metatarsals than metacarpals, a variety of larger notoungulates have longer metacarpals relative to their metatarsals. The Scarritt Pocket sample of *Scarrittia* metapodials yields a mean Mc III-to-Mt III ratio of 1.84 (n = 3) and suggests an allometry in which the relative metacarpal length increases with body size. The asymmetry of the metapodials is even greater in *Homalodotherium*, in which the metacarpals have greater than twice the length of the metatarsals (Mc III/Mt III = 2.26).

67. Radial facet of lunar extent: (0) extends over the dorsal surface of the lunar, to a region at least half way down the body of the lunar in dorsal view; (1) radial facet of lunar restricted to the proximal end of the element so that less than half of the dorsal surface of the lunar is devoted to the facet.

Since the time of Matthew (1937) the degree to which the radial facet covered the lunar has been used as an indication of the degree of wrist extension. In manual plantigrady, greater dorsal coverage of the radial facet is expected, whereas in digitigrade taxa the facet is more limited to the distal surface.

68: Unciform facet angle: (0) distal articulation transverse, with facet for Mc V (if present) at an angle less than 30° to Mc IV facet; (1) facet for Mc V at an angle nearly 45° to Mc IV facet.

69. Ungual phalanx of manus digits compression: (0) lateromedially compressed; (1) dorsopalmar compression, but distal region subequal in width to proximal; (2) hooflike phalanx, distal region wider than proximal.

70. Apex of ungual phalanx of manus, fissure presence/absence: (0) absent, distal apex pointed or rounded, without median fissure; (1) present, median fissure at distal apex.

71. Suprapatellar medial femoral ridge presence/absence: (0) absent; (1) present.

The femora of cf. *Elmerriggsia fieldia* and *Anayatherium* cf. *A. fortis* have distinctive medial ridges of the distal region of the femoral shaft, just proximal to the elongated medial ridge of the patellar groove (medial trochlear ridge). We have not observed this state in any other notoungulates, not even the leontiniid, *Scarrittia*, but the preservation of the region of the femora of this taxon is so poor that we cannot confidently score its presence or absence.

72. Number of digits of the pes: (0) pes pentadactyl, though Mt I may be reduced; (1) tetradactyl, Mt I absent; (2) tridactyl, Mt I absent and Mt V absent or reduced to tarsallike element. (See fig. 12 regarding chars. 72–83).

73. Dorsal prominence of calcaneum orientation: (0) oblique orientation; (1) orthogonal orientation.

74. Calcaneal fibular facet size: (0) small or absent; (1) large.

75. Calcaneal fibular facet form: (0) lenticular; (1) subquadrate; (2) wedge shaped, with proximal transverse dimension greater than the distal.

76. Ectal facet of calcaneum or astragalus orientation: (0) horizontal orientation; (1) steeply inclined articulation between calcaneum and astragalus.

77. Calcaneal-navicular articulation development : (0) absent; there is no evidence of a navicular facet of the calcaneum or a calcaneal facet of the navicular (there may be cuboastragalar contact [i.e., "alternating tarsus"]); (1) present; a small thin articular surface is present at the distal calcaneum that is not due to distal astragalar articulation but has evidence of being due to navicular contact; (2) well-developed navicular facet is present, indicating a strong "reverse alternating" tarsus.

A distinctive feature of the notoungulate tarsus is that it lacks cuboastragalar contact. In some taxa there is actually some to considerable overlap of the calcaneum with the navicular, a condition that Cifelli (1993) called a "reverse alternating tarsus." This is in contrast to the cuboastragalar articulation of the typical "alternating tarsus." Although it has been suggested that the "reverse alternating tarsus" may be a synapomorphy for advanced Toxodontia (Cifelli, 1993) we note that this state occurs in some typotheres (e.g., *Protypotherium* and *Federicoanaya*), as well as lagomorphs and arctostylopids (Shockey and Anaya, 2008).

78. Astragalar foramen (superior): (0) present, foramen is present within the fossa separating the astragalar trochlea with that of the flexor groove; (1) absent.

79. Groove for tendon of flexor hallicus longus (or other flexor tendon) development: (0) present; (1) united to the astragalar trochlea as a plantar component of the astragalar trochlea (Wang, 1993; Shockey and Flynn, 2007).

80. Neck of astragalus shape: (0) neck is well defined, being constricted behind the astragalar head and having a definable length between the head and astragalar body; (1) very short neck with little or no constriction behind the head, which lies very close to the body of the astragalus.

81. Astragalar head shape: (0) subspherical head that does not cover the lateral body in distal view (not expanded laterally); (1) ovoid, with head expanded laterally beyond the midpoint of the body in distal view; (2) teardrop shaped, due to lateral and plantar expansion of the head.

82. Proximomedial astragalar buttress of navicular presence/absence: (0) astragalar buttress present; (1) absent.

In archaic notoungulates and typotheres (except interatheriids) the navicular has a distinctive proximomedial process that articulates with the medial head of the astragalus. Its position is suggestive of the tibiale of rodents (Sinclair, 1909) and *Arctocyon* (Matthew, 1937), which may be the source of this distinctive navicular process (i.e., "tibiale" fused to navicular).

83. Symmetry of trochlea ridges of astragalus: (0) symmetrical, lateral and medial trochlear ridges subequal in height; (1) asymmetric, lateral trochlear ridge distinctly higher than medial.

RESULTS

Phylogenetic Analyses

In order to generate phylogenetic hypotheses regarding the two new leontiniids described in this work and the placement of the Leontiniidae among the Notoungulata, a character-taxon matrix consisting of 27 notoungulates (including 12 leontiniids) and 83 craniodental and postcranial characters was analyzed in PAUP 4.0b10. Three subsets of this character-taxon matrices were derived from this larger matrix. The first two varied the taxonomic composition of the matrix, whereas postcranial characters were excluded from the third. The first analysis, the "Toxodontian" analysis, including only notoungulates traditionally referred to the Toxodontia (sensu Simpson, 1945; Cifelli, 1993) for the ingroup. The henricosborniid *Colbertia magellanica* served as the outgroup for all three analyses. The toxodontian ingroup taxa included leontiniids, toxodontids, notohippids, isotemnids, and a homalodotheriid. Otherwise, taxa traditionally referred to the Typotheria were excluded from this "Toxodontian" analysis. The second analysis, the "Typotheres included" analysis, included all the toxodontians plus five typotherian species (two interatheriids, a hegetothere, and two mesotheriids). All 83 characters were used in these first two analyses. The third analysis included all 27 notoungulates, but excluded all 41 of the postcranial characters. This was accomplished in order to estimate the influence of postcranial characters on the results of the first two analyses. A heuristic search was used in parsimony analyses in all analyses. Starting trees were obtained by stepwise addition with the tree bisection-reconnection branch-swapping algorithm.

Results of the "Toxodontian" Analysis: The "toxodontian" analysis yielded 90 most parsimonious trees, each 156 steps long. The strict consensus tree is shown in figure 13. Indices (excluding uninformative characters) were as follows: Consistency index (CI) = 0.6054; homoplasy index (HI) = 0.3946; retention index (RI) = 0.7671; and rescaled consistency index (RC) = 0.4819. Synapomorphies of selected nodes in figure 13 are discussed below.

Colpodon Clade (Node A, fig. 13): The two species of *Colpodon* form a monophyletic clade nested within a monophyletic Leontiniidae, a group that in this analysis is shown to include only taxa traditionally regarded as leontiniids (Node C). The relatively thin, upper premolar (P2–4) protoloph, recessed from the mesiolingual cingulum (#19[1]) is an unequivocal synapomorphy for *Colpodon*. Equivocal synapomorphies include: absence (reduction: character state change 2→1) of caniniform incisor (#3[1]); mesiolingual face of upper premolar protoloph without connecting ridge (#24[0]); and absence of labial cingulum of lower incisors (33[1]).

"Tropical Clade" (Node B): The strict consensus resolves a "Tropical Clade" of leontiniids, sensu Villarroel and Colwell Danis (1997); however, the mid high-latitude species of *Colpodon* also are in this clade, more closely related to tropical *Huilatherium* than any are to the other tropical taxon (*Taubatherium*), whereas *Colpodon* grouped with *Ancylocoelus* in the Villarroel and Colwell Danis (1997) analysis. No unequivocal synapomorphies define this clade, but equivocal synapomorphies include: absence of canines (#2[1]), absence of cingulum of P1–3 (#16[1]), and absence of cingulid of p2, but its presence on p4 (#36[1]). No monophyletic "Patagonian" clade (sensu Villarroel and Colwell Danis, 1997) is resolved in the "Toxodontian" analysis.

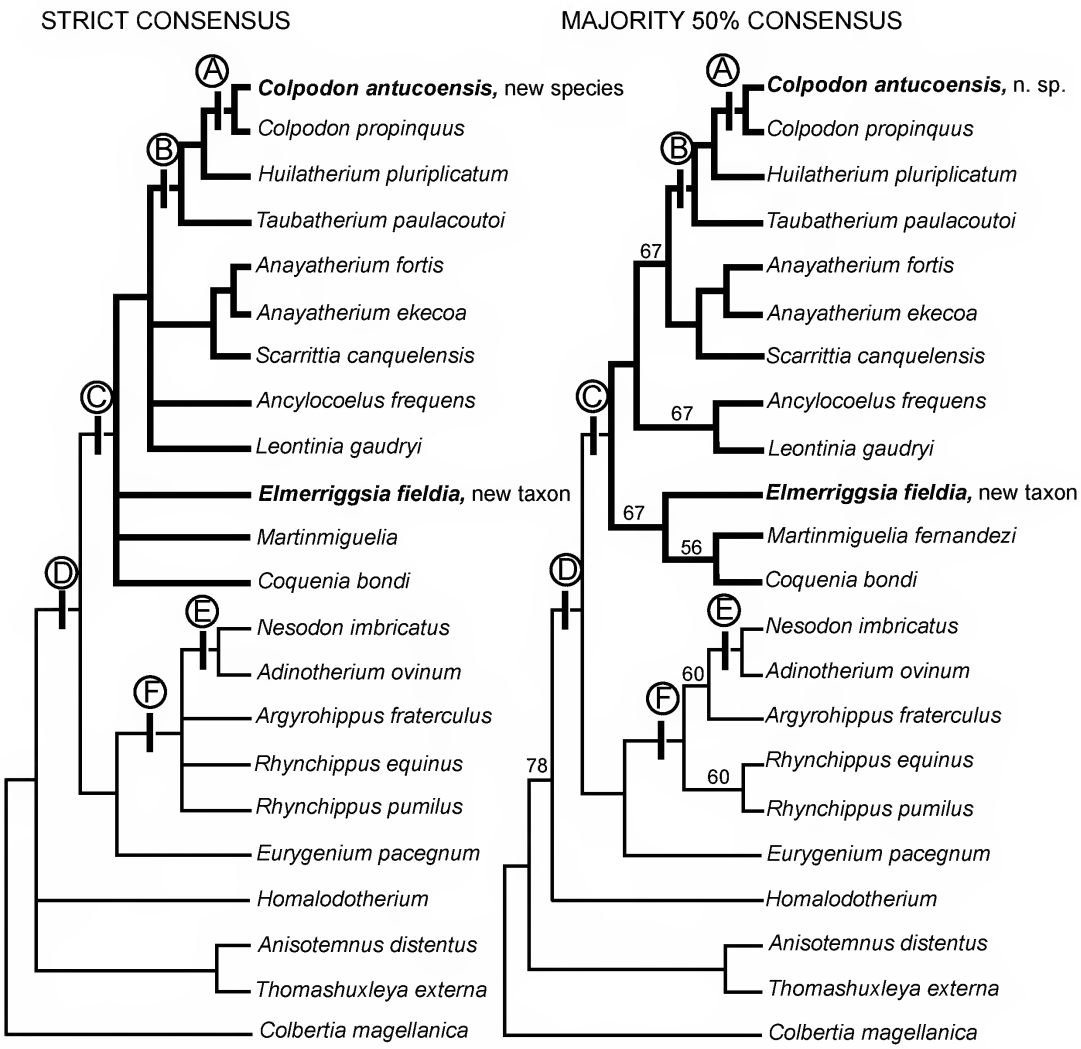


FIGURE 13. Cladogram of the "Toxodont" analysis. Strict consensus (left) and majority 50% consensus of the "Toxodont" phylogenetic analysis. Nodes: **A,** *Colpodon;* **B,** "Tropical clade"; **C,** Leontiniidae; **D,** "advanced Toxodontia"; **E,** Toxodontidae; **F,** "notohippid" + Toxodontidae. Numbers at nodes represent percent support when support is less than 100%.

Leontiniidae (Node C): This node includes only taxa that traditionally have been regarded as leontiniids (sensu Simpson, 1945; Villarroel and Colwell Danis, 1997). Unequivocal synapomorphies diagnosing this clade (and thus, the Leontiniidae) include: strong anterior convergence of the muzzle giving it a V-shaped appearance in palatal view (#1[0]); caniniform i3 (#32[1]); and medial ridge of the cranial face of the distal region of the femur (#71[1]); and a wedge-shaped fibular facet of the calcaneum (#75[2]). Equivocal synapomorphies for leontiniids include: caniniform I2 (#6[1]); enlarged i3 (#31[1]); and branched metaflexid of lower premolars (#34[1]).

The two Eocene taxa (*Coquenia* and *Martinmiguelia*) together with the late Oligocene *Elmerriggsia* appear as an unresolved polytomy of taxa basal to the remaining leontiniids. No

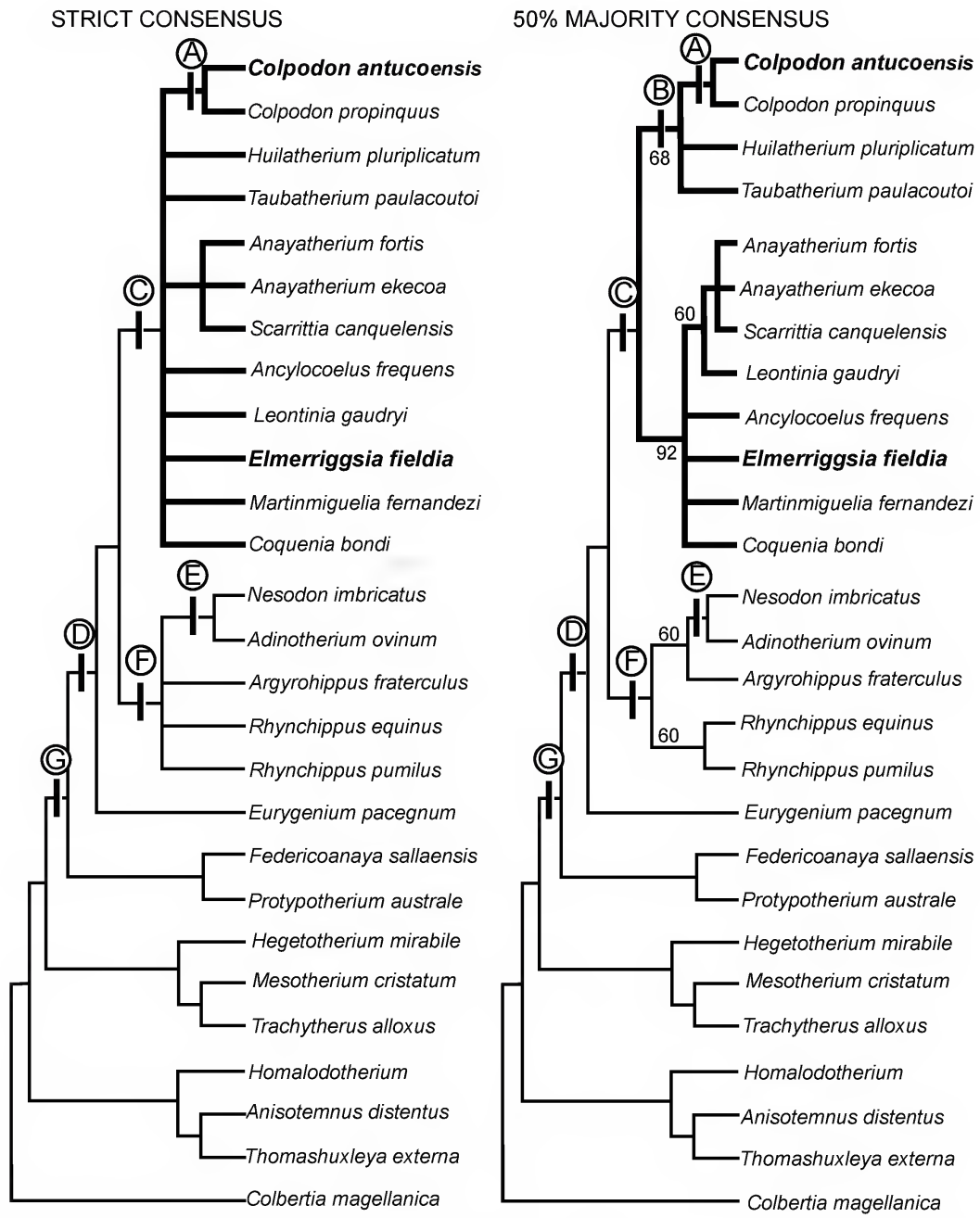


FIGURE 14. Cladogram of the "Typothere included" analysis. Strict consensus (left) and majority 50% consensus of the "Typothere included" phylogenetic analysis. Nodes: **A,** Colpodon; **B,** "Tropical clade"; **C,** Leontiniidae; **D,** "advanced Toxodontia"; **E,** Toxodontidae; **F,** "notohippid"+Toxodontidae (*Eurygenium* excluded); **G,** "advanced Toxodontia" plus interatheriine interatheriids. Numbers at nodes represent percent support when support is less than 100%.

unequivocal synapomorphies unite the remaining leontiniids, but three equivocal synapomorphies weakly suggest such a relationship. These are the tendency for the posterior upper premolar cingulum to rest high on the crown (#17[1]); formation of an intermediate lingual cingulum of the upper premolars (#22[1]); and the formation of a ridge along the mesiolingual face of the upper premolar protoloph (#24[1]).

The presence and placement of the enlarged caniniform upper incisor appears to have some diagnostic value. An enlarged caniniform I2 (#6[1]) appears in the basal leontiniid taxa, as well as *Leontinia* and *Ancylocoelus*. A *Scarrittia-Anayatherium* clade is evidenced by the I1 being the enlarged caniniform incisor (#5[1]). *Colpodon* may be diagnosed by the apomorphic reduction or absence of a large caniniform upper incisor (#3[1]), an apparent loss, changing from #3[2] as implied by its near outgroups having enlarged upper incisors.

"Advanced Toxodontia" (sensu Cifelli, 1993) (Node D): This analysis is consistent with that of Cifelli (1993) in which leontiniids, notohippids (including *Eurygenium*), and toxodontids formed a monophyletic group that excluded homalodotheriids and isotemnids, referred to by Cifelli as "advanced Toxodontia." The numerous unequivocal synapomorphies for the "advanced Toxodontia" identified in this study include: elongated oval fossette between metaloph and distal cingulum of upper molars (#29[1]); absence of the entepicondylar foramen of the humerus (#53[1]); tetradactyl manus (#65[1]); subquadrate form of fibular facet of the calcaneum (#75[1]); "reverse alternating tarsus" with conspicuous articular facets between the navicular and calcaneum (#77[2]); absence of superior astragalar foramen (#78[1]); flexor hallicus longus groove continuous with astragalar trochlea (#79[2]); absence of constricted "neck" of astragalus (#80[1]); transversely elongated ovoid astragalar head (#81[1]); and absence of astragalar "buttress" of the navicular (#82[1]). Equivocal synapomorphies include: placement of the distal cingulum high on the crown of upper premolars (#21[1]); elongated hypoconulid (#41[1]); and presence of entolophid fossettid of lower molars (#41[1]); and supinator crest of humerus small or absent (#52[1]).

The "advanced Toxodontia" (Node D) in this analysis contains two subclades, one that includes the leontiniids (Node C) and another that includes toxodontids (Node E) plus taxa traditionally classified as notohippids. The toxodontids (Node E: *Nesodon* and *Adinotherium*) are recognized by three unequivocal synapomorphies and at least three equivocal derived traits (below). In this analysis, "notohippids" are nonmonophyletic (paraphyletic) as detailed below (fig. 13). *Eurygenium* lacks the derived characters that diagnose Node F, which includes the remaining notohippids (*Rhynchippus* spp. and *Argyrohippus*) the toxodontids. Thus, it is excluded from the unnamed clade at Node F.

Toxodontidae (Node E): The transverse muzzle (#1[2]), hypselodont incisors (#8[1]), and hypselodont molars (#11[1]) appear as unequivocal synapomorphies for the toxodontids *Nesodon* and *Adinotherium*. Equivocal synapomorphies include: procumbent lower incisors (#30[1); enlarged i3 (#31[1]); and the distal radius with a well-developed styloid process (#63[2]). The secondary metacromion of the scapulae of *Nesodon* and *Adinotherium* (#46[1]) may also be a synapomorphy for the Toxodontidae, however, the scapula is so poorly known in the related "notohippids" that the presence/absence of this character state cannot be assessed in these taxa.

Unnamed clade (Node F): The monophyletic Toxodontidae are nested among paraphyletic "notohippids," with the latter in a polytomy as the nearest outgroup to the toxodontids. Unequivocal synapomorphies uniting the "notohippids" *Rhynchippus* spp. and *Argyrohippus* with toxodontids (to the exclusion of *Eurygenium*) include: first crista of upper molars distinct and persistent (#27[1]); articular surface of radial head subrectangular and undulating (#59[1] and #60[1]); tridactyl manus (#65[2]); Mc V facet of unciform at sharp angle to Mc IV facet (#68[1]); and tridactyl pes (#72[2]). *Eurygenium* lacks the half dozen unequivocal synapomorphies that characterize Node F, which includes the remaining taxa traditionally considered to be notohippids (*Rhynchippus* and *Argyrohippus*) plus the toxodontids; thus, it is excluded from the clade at Node F.

Other results from "Toxodontian Analysis": The strict consensus analysis did not demonstrate any special relationship of *Homalodotherium* with the "advanced Toxodontia." Instead, *Homalodotherium* and the isotemnids (*Anisotemnus* and *Thomashuxleya*) formed two branches of the tritomous toxodontian ingroup, with the "advanced Toxodontia" forming the third. The majority rule consensus analysis, however, placed *Homalodotherium* as sister to the "advanced Toxodontia" in 78% of the trees. When only dental characters were considered (postcranial characters deleted), *Homalodotherium* nested among the leontiniids.

The results of an Adams consensus analysis of the "Toxodontian matrix" were identical to those of the strict consensus (fig. 13). The only differences between these analyses and those of a 50% majority-rule consensus were that the majority-rule consensus suggested special relationships between *Coquenia* and *Martinmiguelia* as well as *Leontinia* and *Ancylocoelus*. The majority-rule consensus also resolved a monophyletic *Rhynchippus* (*R. equinus* and *R. pumilus*), and resolved the polytomy at Node F, placing *Argyrohippus* as the nearest outgroup to toxodontids.

Results of the "Typotheres Included" Analysis: The "Typotheres included" analysis was based on the same character matrix as the "Toxodontian Analysis," with five additional species included (two interatheriids, two mesotheriids, and a hegetothere). This analysis yielded 2635 most parsimonious trees, each 195 steps long. The strict consensus is shown in figure 14. Indices (excluding uninformative characters) were: CI = 0.5260; HI = 0.4740; RI = 0.7641; and RC = 0.4079.

Leontiniidae (Node C. fig. 14): The strict consensus of the "typotheres included" matrix places all the traditional leontiniid taxa within a monophyletic group, but otherwise shows little resolution of relationships among leontiniids (fig. 14). These taxa form a polytomy with the exception of the pairing of the two species of *Colpodon*, and the linkage of the two *Anayatherium* species in a polytomy with *Scarrittia* (fig. 14). When a 50% majority-rule consensus is applied, monophyletic Patagonian versus Tropical + *Colpodon* subclades are resolved. Unlike for the "toxodont" analysis, the 50% majority-rule consensus of this analysis identifies both groups as monophyletic (the Patagonian taxa were paraphyletic to a Tropical + *Colpodon* clade in the "toxodont" analysis of fig. 13).

The synapomorphies uniting the leontiniid taxa are the same as in the "Toxodontian analysis," except that the mesodont condition of leontiniids equivocally appears as a reversal (#12[1],

changed from the near outgroup condition of #12[2], hypsodont to mesodont).

Interatheriidae + "advanced Toxodontia" clade (Node G): The most unconventional result of this analysis is that the typothere taxa are paraphyletic to the "advanced Toxodontia." This is due to several postcranial characters that the interatheriine interatheriids (*Federicoanaya* and *Protypotherium*) share with "advanced toxodontians" (*Eurygenium*, other "notohippids," toxodontids, and leontiniids). Unequivocal synapomorphies uniting the interatheriids with *Eurygenium*, leontiniids, the "notohippids" *Rhynchippus* and *Argyrohippus*, and toxodontids include: tetradactyl manus (#65[1]); quadrate fibular facet of the calcaneum (#75[1]); calcaneal-navicular contact (#77[1]); and union of the groove for the tendon of the flexor hallucis longus with the astragalar trochlea (#79[1]). Steeply inclined ectal facet of the astragalus and calcaneum (#76[1]) is an equivocal synapomorphy of this group (the character state in leontiniids is #76[0]).

Inclusion of the typotheres yields *Eurygenium* as the earliest diverging advanced "toxodontian," as the nearest outgroup to leontiniids plus the clade of the remaining "notohippids" + toxodontids. Unequivocal synapomorphies that unite *Eurygenium* with the other toxodontians include: absence of entepicondylar foramen of the humerus (#54[1]); short astragalar neck (#80[1]); transversely elongated astragalar head (#81[1]); absence of astragalar buttress of the navicular (#82[1]); and formation of fossette of the molars between the metaloph and the posterior cingulum (#29[1]).

In this analysis members of "advanced Toxodontia" are united by the unequivocal synapomorphies of oblique outline of distal radius (#62[1]) and well-developed articular facets for navicular-calcaneum articulation (#77[2]). Equivocal synapomorphies include enlarged i3 (#30[1]) and entolophid fossette of lower molars (#41[1]).

Results of "Postcranials Excluded" Analysis: The analysis that excluded the postcranial characters yielded 31 most parsimonious trees, each 105 steps long. Indices (excluding uninformative characters) were as follows: Consistency index (CI) = 0.5049; homoplasy index (HI) = 0.4951; retention index (RI) = 0.7927; and rescaled consistency index (RC) = 0.4077.

A strict consensus tree of this modified matrix resolves two major ingroup nodes, one of which contains a monophyletic Typotheria (mesotheriids, interatheriids, and a hegetothere) and a monophyletic Toxodontia composed of "notohippids" and toxodontids, but not the leontiniids. In this "postcranials excluded" analysis, leontiniids nested within isotemnids and the homalodotheriid.

DISCUSSION

Colpodon antucoensis: Biogeography and Age

The discovery of *Colpodon antucoensis,* new species, at Laguna del Laja, Chile, extends the geographic range of *Colpodon*. Species of *Colpodon* were previously known only from various localities in Chubut and Rio Negro provinces of central Patagonia, Argentina. This geographic range extension is modest (see map, fig. 1). At about 37.5° S and 71.3° W, Laguna del Laja is roughly 360 km northwest of the Colhuehuapian Paso Cordoba locality of Rio Negro, Argentina, which previously had been the northernmost record of *Colpodon*.

The presence of *Colpodon* at the Estero Correntoso locality of Laguna del Laja initially suggests a Colhuehuapian age for these lower horizons of the Cura-Mallín Formation (Tcm_1). Indeed, *Colpodon* has been used as the index fossil of the Colhuehuapian since Ameghino first recognized the beds as the "couches à *Colpodon*" (Ameghino, 1902). However, consideration of radioisotopic ages available for the lower Cura-Mallín and for fossil taxa coeval to the holotype of *C. antucoensis*, as well as noting that this is a new species of *Colpodon* distinct from Patagonian forms, suggests that caution is warranted in assigning a faunal age to Tcm_1.

Horizons bracketing the type specimen of *C. antucoensis* yield $^{39}Ar/^{40}Ar$ ages of 19.25 ± 1.22 Ma above and 19.53 ± 0.60 Ma below (fig. 4), thus constraining its age at ~19.5 Ma (corrected to ~19.8 Ma for the revised Fish Canyon Tuff age). The age of the Colhuehuapian SALMA is best constrained by radioisotopic and paleomagnetic studies at its type locality at the Gran Barranca (Ré et al., 2010a, 2010b). Ré et al.'s preferred paleomagnetic interpretation (using the calibration of radioisotopic ages) from the Colhue-Huapi Member is that the "Lower Fossil Zone," producing the Colhuehuapian SALMA fauna, is in Chron C6An.1n (Ré et al., 2010b). This suggests an age of 20.0 Ma–20.2 Ma for the Colhuehuapian SALMA, although its full temporal span remains unclear (tentatively estimated at 19–21 Ma by Flynn and Swisher, 1995). This ~20 Ma age estimate is only slightly older than the age (~19.8 Ma) of *C. antucoensis* in the Tcm_1 of Laguna del Laja.

Overlying the Colhuehuapian SALMA fauna, in the "Upper Fossil Zone" of the Colhue-Huapi Member at Gran Barranca, is a fauna recently recognized as being "Pinturan" (Kramarz et al., 2010), an informal biochron considered to be intermediate in age between Colhuehuapian and Santacrucian SALMA faunas (Vucetich et al., 2005; Carlini et al., 2005). Ré's preferred interpretation of radioisotopic-paleomagnetic results in that section is that the "Upper Fossil Zone" containing the "Pinturan" fauna lies within C6n, suggesting an age range from about 19.7 to 18.7 Ma (Ré, 2010b). Recognizing that "Pinturan" localities outside of Gran Barranca have yielded younger radiometric ages (~17.5 Ma; Fleagle et al., [1995]), Kramarz et al. (2010) used the younger extreme of the age for Chron 6n as the older extreme of the suggested "Pinturan" age, proposing that the "Pinturan" ranged from 18.75 to 16.5 Ma. Croft et al. (2007) extended the beginning of the Santacrucian SALMA to be as old as ~19 Ma, based on dates associated with the Chucal Fauna of northern Chile (correlated to the Santacrucian). This suggests either that the "Pinturan" is a very short time interval preceding the Santacrucian SALMA (consistent with the results of Ré, 2010b, but not with the younger estimates of Fleagle et al., 1995, and Kramarz et al., 2010), or that it falls within the Santacrucian SALMA.

The few other taxa identified to date from the same interval in the Estero Correntoso section (Tcm_1) at Laguna del Laja suggest a post-Colhuehuapian age for *Colpodon antucoensis*. For example, a lagostomine chinchillid is known from Tcm_1 of Estero Correntoso and is otherwise known only from Santacrucian or younger faunas (Flynn et al., 2008). A sloth from Estero Correntoso is referable to *Nematherium* (cf. *N. angulatum* or sp. nov.; Flynn et al., 2008: fig. 4d). *Nematherium* is best known from the Santacrucian, but it also occurs in the "Pinturas" fauna of the Upper Fossil Zone of the Colhue-Huapi Member of Gran Barranca (Kramarz et al., 2010). The only taxon that occurs at both Estero Correntoso and in a known Colhuehuapian

age fauna, aside from *Colpodon*, is *Protypotherium* sp. However, the age range of this interatheriid notoungulate is so great (extending from the Colhuehuapian and "Pinturan" up into the Chapadmalalan and possibly younger [Flynn et al., 2008]) that it has no utility in helping to discriminate time based on faunal similarities.

Thus, the radioisotopic age and taxa coeval with *Colpodon antucoensis* suggest that this species of *Colpodon* is possibly a little younger than the faunal interval that once carried its generic name—"couches à *Colpodon*." Since *Colpodon* is the only known post-Deseadan leontiniid of southern South America, its temporal range extension also extends the temporal record of leontiniids in southern South America. Only the Laventan-aged *Huilatherium* of northern South America (Colombia) is younger (Villarroel and Colwell Danis, 1997).

Phylogenetic Considerations

"Tropical" vs. "Patagonian" Clades: Our phylogenetic analyses provide weak support for the "Tropical" clade of leontiniids proposed by Villarroel and Colwell Danis (1997). The composition of that clade, however, differs in this study in that higher-latitude *Colpodon* is included in a clade with the "tropical" *Taubatherium* and *Huilatherium* (from Brazil and Colombia, respectively). All remaining leontiniids, including the low-latitude species of *Anayatherium* and the extra-Patagonian Mustersan (late Eocene) *Coquenia* and *Martinmiguelia,* are paraphyletic with respect to the "Tropical" clade in all our analyses, except in the 50% majority rule consensus of the "Typotheres included" analysis. In that latter analysis both a "Tropical" clade and a second monophyletic high-latitude clade share a similar composition to the "Patagonian" clade of Villarroel and Colwell Danis (1997). Three equivocal synapomorphies support the monophyly of the "Patagonian" clade in this 50% majority-rule consensus. Two of these appeared more frequently in other taxa than in the "Patagonian" clade. Thus, this lack of compelling evidence for a monophyletic "Patagonian" clade and the fact that half the taxa that form the group are not from Patagonia renders the concept unuseful. We consider it more likely that the "Tropical" taxa plus species of *Colpodon* form a natural group. Such a clade, with *Colpodon* nested among the lower-latitude near outgroups, *Taubatherium* and *Huilatherium* (Brazilian and Colombian taxa respectively), suggests an extra-Patagonian origin of *Colpodon*.

Dental Plasticity

It is of interest that an enlarged caniniform incisor is nearly ubiquitous in leontiniids, but the particular upper incisor that is enlarged is variable, although i3 is invariably the enlarged lower incisor. The enlarged, sometimes tusklike, upper incisor is the I2 in *Coquenia, Martinmiguelia, Leontinia, Elmerriggsia*, and *Ancylocoelus*, but I1 is enlarged instead in *Scarrittia* and *Anayatherium*.

Cifelli (1993: #1[1]) defined the character state of enlarged incisor, regardless of its particular locus (I1 or I2), in his phylogenetic analysis of "advanced Toxodontia." Implicit in the use of such a character, where it does not matter which particular incisor has the derived state, is the assumption that the enlargement (of the anteriormost "incisiform") is homologous even

though the feature manifests itself at a different tooth locus. Two competing arguments can be made regarding such a definition of a derived state: (1) since the derived form occurs at two different tooth loci they should *not* be regarded as homologous, but rather as independent transformations from the plesiomorphic form, or alternatively, that (2) they should not be assumed to be independent, since the structures in question are close (adjacent) serial homologs, and the developmental influences that affect one locus do not need to be "reinvented" to affect another. In the latter scenario, a small change in the way in which the derived developmental process is executed may manifest itself at a slightly different location, and it is the inferred developmental change that is homologous.

Such "frame shifts" have been documented in development and evolution, (e.g., the putative shift in the manual digits of nonavian dinosaurs to those of birds [Wagner and Gauthier, 1999]). We regard it as both biologically plausible and most parsimonious to conclude that the gene expression for an enlarged upper incisor shifted from I2 to I1 in the common ancestor of *Anayatherium* and *Scarrittia*. The alternative hypothesis (that the two character states are independent) requires the independent reduction of I2 and a simultaneous (or nearly so) independent evolution of a large I1 in *Anayatherium* and *Scarrittia*. The nesting of *Anayatherium-Scarrittia* species among leontiniids having enlarged I2, when either means of scoring was used, supports this assertion.

Postcranial Characters in the Phylogenetic Analysis

The inclusion of postcranial data strongly influenced the tree topology. For example, when we excluded the postcranial characters, leontiniids and the homalodotheriid appear as sister taxa nested among isotemnids forming a clade, separate from the "advanced Toxodontia" and typotheres. Such a leontiniid, homalodotheriid, isotemnid group is reminiscent of the Entelonychia of Ameghino (1895). We note that, indeed, the dentitions of homalodotheriids and leontiniids are nearly identical. The relative height of the posterior cingulum is about the only difference between cheek teeth in the two groups (Patterson, 1934). The incisors, too, are nearly identical to each other, with both homalodotheriids and leontiniids having somewhat caniniform incisors with strong labial and lingual cingulae. Scott (1912b), however, expressed serious doubts regarding a close relationship between leontiniids and homalodotheriids, due to differences in the tarsus in each. He noted that a proximal tarsus referred to *Leontinia gaudryi* by Gaudry (1906; denoted as "*Colpodon gaudryi*") was similar to that of the toxodontid *Nesodon*, but quite unlike that of *Homalodotherium*. The results of our analyses with postcranials strongly support Scott's rejection of a close homalodotheriid-leontiniid relationship.

Also, our analyses demonstrate that several characters of the postcranial skeleton are useful in recognizing taxonomic groups of notoungulates. Several of these of the scapula, manus, and pes are illustrated in figures 10, 11, and 12.

A hypothesis for a morphological transition series relevant to the leontiniids involves the pes (fig. 12). The "advanced Toxodontia" (sensu Cifelli, 1993; = Leontiniidae + "Notohippidae" + Toxodontidae) are characterized by orthogonal orientation of the dorsal prominence of the calcaneum (#73[1]), robust fibular facet (#74[1]) with quadrate form (#75[1]), and (excepting

leontiniids) by steeply inclined ectal articulation of the proximal tarsals (#75-6[1]). These character states also occur in interatheriids (see also Shockey and Anaya, 2008) and are evident in the interatheriine interatheriids *Federicoanaya* and *Protypotherium* analyzed in this study. Additionally, the navicular and calcaneum make contact in all these taxa (reverse alternating tarsus, sensu Cifelli, 1993) and a distinctive facet develops in leontiniids, toxodontids, and some "notohippids" (e.g., *Pascualihippus* [Shockey and Anaya, 2008], but not *Eurygenium* [this study]). Leontiniids differ from interatheriids, "notohippids," and toxodontids by their less inclined ectal facets of the calcaneum and astragalus; that is the astragalus more strongly overlies the calcaneum, where it is known in leontiniids. The contact between the two proximal tarsal elements of interatheriids, "notohippids," and toxodontids may be characterized as side by side, rather than overlapping. The foot of the interatheriids *Federicoanaya* and *Protypotherium* is distinct from those of other "typotheres" (Shockey and Anaya, 2008). Like the traditional "advanced Toxodontia" their upper ankle joint has strong fibular-calcaneal contact resulting in a large, orthogonal fibular facet of the calcaneum. The upper ankle joint of the mesotheriids (*Trachytherus*, *Mesotherium*) and *Hegetotherium* have weaker fibular-calcaneal contact, oblique dorsal prominence of the calcaneum, and the astragalus overlies the calcaneum, with their ectal facets more horizontal than those of the interatheriids, "notohippids," and toxodontids (fig. 12).

"Uninformative" Characters

Some characters identified in this study were invariant in Notoungulata, and thus "uninformative" in terms of their utility in estimating phylogenetic relationships among notoungulates, so were not discussed in the final analysis. However, these characters may prove useful in resolving interrelationships among a broader suite of endemic South American "ungulates" and other eutherians. Examples of these characters include the fused mandibular symphysis, the absence of separate centrale of manus, and the absence of any "alternating" tarsus; that is, one in which the astragalus contact the cuboid. We also found a fused mandibular symphysis to be ubiquitous among notoungulates, occurring also in groups not included in our cladistic analysis (due to lack of postcranials) including notostylopids, henricosborniids, and oldfieldthomasiids. However, this derived trait may not be a synapomorphy for only Notoungulata, as we also found mandibular symphyses invariably fused in astrapotheres (*Astrapotherium*, *Parastrapotherium*, *Trigonostylops*) and litopterns (e.g., *Theosodon*, proterotheriids). Among South American native ungulates, it is unfused only in Pyrotheria (*Pyrotherium*) and Xenungulata (*Carodnia*). Likewise, where known, all notoungulates lack a centrale of the wrist, and every scaphoid we encountered had a magnum process that may represent the fusion of the centrale to the scaphoid. Further, we did not encounter any notoungulate having an "alternating" tarsus (i.e., none showed cuboastragalar contact). The tarsals were either serial (e.g., *Trachytherus*) or had the "reverse alternating" form (sensu Cifelli, 1993) in which the calcaneum and navicular make contact (e.g., toxodontids and leontiniids; fig. 12). Among the extinct, endemic South American ungulates, a robust alternating tarsus is found among pyrotheres (Shockey and Anaya, 2004).

SUMMARY AND CONCLUSIONS

In this work we describe two new leontiniids, evaluate their relationships among other leontiniids, and reconstruct the relationship of leontiniids to other notoungulates. Taxa included in these analyses were selected for the availability of postcranial elements so that these skeletal characters, often excluded from analyses, could be included in this more comprehensive phylogenetic analysis. The findings of our study may be summarized as follows:

• Leontiniid of Laguna del Laja: *Colpodon antucoensis* is a new species from Estero Correntoso, near Laguna del Laja, in the central Andes of Chile. Its age is estimated to be about 19.8 Ma. This age is a little younger than the type Colhuehuapian SALMA fauna of from the Gran Barranca (20.0–20.2 Ma [Ré, 2010b]), yet older than the Kramarz et al. (2010) age estimate of the range of the transitional post-Colhuehuapian/pre-Santacrucian "Pinturan" fauna (18.75 to 16.5 Ma), as well as the expanded age estimate for the Santacrucian by Croft et al. (2007; to as old as ~19 Ma). However, since there is no known hiatus between the "Lower Fossil Zone" and the "Upper Fossil Zone" of the Colhue-Huapi Member (≈ Colhuehuapian SALMA assemblage and "Pinturas" fauna respectively; Ré et al., 2010b) and since the favored paleomagnetic interpretation places the "Upper Fossil Zone" ("Pinturas" fauna) in C6n (19.7 to 18.7 Ma), we suggest that the Colhuehuapian-to-Santacrucian faunal changes began by 19.8 Ma. Such a hypothesis is consistent with other biostratigraphic evidence from the Laguna del Laja sequence, including the presence of Santacrucian and "Pinturan" taxa like *Nematherium* and the lagostomine chinchillid in the lower horizons at Laguna del Laja (Flynn et al., 2008). Thus, *Colpodon antucoensis* may extend both the geographic and age range of species of *Colpodon*, which has previously been known only from Chubut and Río Negro provinces of Argentina (central Patagonia), and only from the Colhuehuapian SALMA (= "couches à *Colpodon*").

• Laguna del Laja Sequence. Implicit in the age hypothesis above for the type locality of *Colpodon antucoensis* is that the Laguna del Laja localities provide important paleontological data regarding the faunal turnover that occurred between the Colhuehuapian and Santacrucian SALMAs. Tcm_1 is but the lowest of a series of fossil-bearing horizons. These have already been shown to contain a mixture of taxa that are also known elsewhere from Colhuehuapian, "Pinturan," and Santacrucian faunas (Flynn et al., 2008).

•New Deseadan Leontiniid: *Elmerriggsia fieldia* is a new leontiniid taxon from the Deseadan SALMA Pico Truncado locality of southern Patagonia, Chubut, Argentina. This medium-sized leontiniid tends to be one of the more basal leontiniids in our analyses. This taxon also extends the recognized number of leontiniids of the Deseadan of Patagonia, which had already been known to have the greatest diversity of the group (Ribeiro et al., 2010).

• Leontiniid Biogeography: Eocene (Mustersan SALMA) leontiniids are known only from northwestern Argentina (*Coquenia* and *Martinmiguelia*), whereas the group's peak diversity is in the Deseadan of Patagonia (leontiniids are present, but scarce in the Deseadan of Bolivia; Shockey, 2005). Our phylogenetic analyses weakly supports the "Tropical" clade suggested by Villarroel and Colwell Danis (1997); however, the composition of this clade differs, with higher latitude species of *Colpodon* appearing to have a close relationship with the low-

latitude leontiniids, *Taubatherium* and *Huilatherium*. All remaining leontiniids, even the relatively low-latitude *Anayatherium* species and the Mustersan SALMA taxa from northwestern Argentina, are paraphyletic with respect to the proposed "Tropical" clade. The paraphyletic nature of the putative "Patagonian clade" along with the fact that several of these taxa are not from Patagonia makes the concept unuseful. The absence of known leontiniids in the Mustersan of Patagonia and the presence in northwestern Argentina suggests an extra-Patagonian origin of leontiniids.

• Postcranial Contributions to Phylogenetic Analyses: Inclusion of postcranial elements in our analysis profoundly changed the tree topologies. Most unconventional is the finding that interatheriids (represented by *Federicoanaya* and *Protypotherium*) and traditional "advanced Toxodontia" share a number of postcranial synapomorphies (Node G of fig. 14), including: tetradactyl manus, a robust, tricontact (strong fibular-calcaneal articulation) upper ankle joint and a "reverse alternating" tarsus (sensu Cifelli, 1993). The current analysis suggests that this specialized ankle in interatheres and "advanced Toxodontia" is homologous. We note that the only significant difference in the ankles of these two groups is that the interatheriids (*Federicoanaya* and *Protypotherium*) have elongated astragalar necks (regarded as plesiomorphic in our analysis), whereas the "advanced Toxodontia" (including *Eurygenium*) astragali have short necks.

The implications of such an interatheriid-toxodont clade are not trivial. It unconventionally suggests that typotheres are paraphyletic to "advanced Toxodontia," challenging long-standing ideas regarding a close leontiniid-isotemnid relationship. This interatheriid–"advanced Toxodontia" relationship is a falsifiable hypothesis that should be tested with further analyses that include more characters and features from other systems (e.g., basicranial, auditory) and, it is hoped, with the addition of postcranial elements in key notoungulate taxa that are currently unknown (e.g., archaeohyracids and "notopithecine" interatheriids). We note that the homoplasy vs. homology conflict between the postcrania and dentitions would be undetectable (except in a qualitative fashion [see Shockey and Anaya, 2008: fig. 7.11]) when postcranial elements are not included in phylogenetic analyses. Such conflicts between systems may be inevitable, but should not be ignored, and systematists should strive to incorporate all potentially phylogenetically informative characters to develop the most comprehensive and robustly tested hypotheses of relationships. Ultimately, *all* the bones can help illuminate the phylogenetic histories and perhaps even something regarding the lives of these curious South American animals.

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APPENDIX 1

CHARACTER-TAXON MATRIX

Letters represent multistate characters: a = 0/1; b = 1/2.

Taxon / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Colbertia magellanica	?	0	0	0	0	0	0	0	0	0	0	0	0	?	0	2	0	2	0	0	0	0	1	0	1
Anisotemnus distentus	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Thomashuxleya externa	1	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	?	0	0	0	0	0	0	0
Coquenia bondi	0	0	2	1	0	1	1	0	0	0	0	0	0	0	a	a	?	0	0	0	0	0	0	0	0
Martinmiguelia fernandezi	0	0	2	1	0	1	1	0	0	0	0	?	0	0	?	0	?	?	?	0	?	?	?	?	?
Taubatherium paulacoutoi	0	?	2	?	?	?	?	0	?	0	0	1	0	?	a	1	1	?	0	0	1	0	?	?	1
Ancylocoelus frequens	0	0	2	?	0	1	1	0	?	0	0	1	0	1	1	0	0	1	0	0	1	1	0	a	1
Leontinia gaudryi	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	1	2	0	0	1	1	1	1	1
Elmerriggsia fieldia	0	0	2	?	0	1	1	0	0	0	0	1	0	0	1	0	0	2	0	0	0	0	1	0	0
Scarrittia canquelensis	0	0	2	1	1	0	1	0	0	0	0	1	0	0	1	0	1	2	0	0	1	1	0	a	1
Anayatherium ekecoa	0	2	2	1	1	0	1	0	0	0	0	1	0	0	1	0	1	2	0	0	1	1	1	?	1
Anayatherium fortis	0	0	2	1	1	0	1	0	0	0	0	1	0	?	1	0	1	2	0	0	1	1	1	1	1
Huilatherium pluriplicatum	0	2	2	?	?	?	?	0	1	0	0	1	0	0	1	1	1	0	0	0	?	?	0	1	1
Colpodon propinquus	0	1	1	0	0	0	a	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	a	1
Colpodon antucoensis	0	2	1	?	0	0	?	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1
Rhynchippus equinus	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0	2	0	1	0	0	1	0	0	0	1
Rhynchippus pumilus	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0	2	0	1	0	0	1	0	0	0	1
Argyrohippus fraterculus	1	1	1	0	0	0	0	0	1	0	0	2	2	?	0	2	0	1	0	1	1	0	0	0	1
Eurygenium pacegnum	1	0	1	0	0	0	0	0	0	0	0	2	1	0	0	2	0	2	0	1	1	0	0	0	1
Nesodon imbricatus	2	0	1	0	0	0	0	1	0	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	1
Adinotherium ovinum	2	0	1	0	0	0	0	1	0	0	1	2	0	0	0	2	0	1	0	1	1	0	0	0	1
Homalodotherium cunninghami	1	0	a	1	0	0	1	0	0	0	0	1	0	0	1	0	1	2	0	0	0	1	1	0	1
Federicoanaya sallaensis	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	2	0	2	0	1	1	0	0	0	1
Protypotherium australe	0	0	1	0	0	0	0	0	0	0	1	2	1	0	0	2	0	2	0	1	1	0	0	0	1
Hegetotherium mirabile	0	0	1	2	0	0	0	1	0	?	1	2	1	?	0	2	0	2	0	1	1	0	0	0	1
Trachytherus alloxus	0	a	1	2	0	0	0	1	1	0	1	2	2	?	0	2	0	2	0	1	1	0	0	0	1
Mesotherium cristatum	0	2	1	2	0	0	0	1	1	1	1	2	2	?	0	2	0	2	0	1	1	0	0	0	1

Taxon / Character	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Colbertia magellanica	2	0	0	0	?	0	0	?	?	?	?	0	0	?	?	0	0	?	?	?
Anisotemnus distentus	0	0	0	0	?	0	?	?	0	2	2	0	1	1	1	0	0	0	0	0
Thomashuxleya externa	0	0	0	?	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Coquenia bondi	1	0	0	1	0	1	1	0	?	0	0	1	0	0	1	0	0	?	?	?
Martinmiguelia fernandezi	?	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taubatherium paulacoutoi	0	0	0	1	?	?	?	?	1	?	?	1	?	?	?	?	1	?	?	?
Ancylocoelus frequens	1	?	0	1	0	1	1	0	1	0	0	1	0	0	a	1	1	?	?	?
Leontinia gaudryi	2	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1	1
Elmerriggsia fieldia	2	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	?	?	?
Scarrittia canquelensis	2	0	0	1	0	1	1	0	1	0	0	1	0	0	a	1	1	1	1	1
Anayatherium ekecoa	2	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anayatherium fortis	2	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huilatherium pluriplicatum	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	?	?	?
Colpodon propinquus	0	0	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	?	?	?
Colpodon antucoensis	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchippus equinus	1	1	1	1	0	0	0	1	0	0	2	1	0	1	1	1	1	?	?	?
Rhynchippus pumilus	1	1	1	1	0	0	0	1	0	?	2	1	0	1	1	1	1	?	?	?
Argyrohippus fraterculus	1	1	1	1	0	0	0	1	?	2	2	1	0	1	1	1	1	?	?	?
Eurygenium pacegnum	2	0	1	1	0	0	0	1	0	2	2	1	0	1	1	1	0	?	?	?
Nesodon imbricatus	1	1	1	1	1	1	0	1	0	2	2	1	0	1	1	1	1	1	1	1
Adinotherium ovinum	1	1	1	1	1	1	0	1	0	2	2	1	0	1	1	1	1	1	1	1
Homalodotherium cunninghami	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Federicoanaya sallaensis	2	0	1	0	0	0	0	1	0	2	2	1	0	1	1	?	0	?	?	?
Protypotherium australe	2	0	1	0	0	0	0	1	0	2	2	1	0	1	1	?	0	0	0	0
Hegetotherium mirabile	2	0	1	0	1	0	2	1	0	2	2	1	0	1	1	?	0	?	?	?
Trachytherus alloxus	2	0	1	0	1	0	2	1	0	2	2	1	0	1	1	1	0	?	1	1
Mesotherium cristatum	2	0	1	0	1	0	2	1	0	2	2	1	0	1	1	1	0	0	1	1

Taxon \ Character	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
Colbertia magellanica	?	?	?	?	?	?	1	0	0	a	?	1	0	0	0	0	?	?	?	?
Anisotemnus distentus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Thomashuxleya externa	0	1	0	0	0	0	0	0	0	1	?	2	0	0	0	0	?	0	?	0
Coquenia bondi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Martinmiguelia fernandezi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taubatherium paulacoutoi	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?
Ancylocoelus frequens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Leontinia gaudryi	0	1	1	0	0	?	1	1	1	?	?	2	?	0	?	?	?	?	?	?
Elmerriggsia fieldia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Scarrittia canquelensis	0	1	1	0	0	1	1	1	1	0	1	2	0	0	0	0	1	1	1	1
Anayatherium ekecoa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anayatherium fortis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huilatherium pluriplicatum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colpodon propinquus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colpodon antucoensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchippus equinus	?	1	?	0	0	1	1	1	1	0	1	2	0	1	1	1	1	1	0	2
Rhynchippus pumilus	?	1	?	?	?	?	1	1	1	0	?	0	0	?	?	?	?	?	?	?
Argyrohippus fraterculus	?	?	?	?	?	?	1	1	1	0	?	2	0	1	1	?	0	1	?	?
Eurygenium pacegnum	?	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	?	0	0	1
Nesodon imbricatus	1	1	1	0	0	1	1	1	1	a	1	2	0	1	1	1	1	2	0	2
Adinotherium ovinum	1	1	1	0	0	1	1	1	1	?	1	2	0	1	1	1	1	2	0	2
Homalodotherium cunninghami	0	0	?	0	0	1	0	0	?	1	2	0	1	?	?	0	1	?	1	0
Federicoanaya sallaensis	?	?	?	1	1	1	1	0	0	a	0	1	0	0	0	0	?	0	0	1
Protypotherium australe	0	?	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1
Hegetotherium mirabile	?	?	?	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	?	?
Trachytherus alloxus	0	?	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0
Mesotherium cristatum	0	?	1	0	0	1	0	0	0	0	0	?	1	1	1	0	1	0	0	0

Taxon \ Character	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Colbertia magellanica	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	?	0
Anisotemnus distentus	?	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Thomashuxleya externa	?	0	0	?	?	?	?	?	?	?	?	?	0	a	0	0	?	0
Coquenia bondi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Martinmiguelia fernandezi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taubatherium paulacoutoi	?	?	?	?	?	?	?	1	1	2	0	2	?	?	?	?	?	?
Ancylocoelus frequens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Leontinia gaudryi	?	1	?	?	?	1	?	1	1	2	0	?	1	1	1	1	1	1
Elmerriggsia fieldia	?	?	?	?	?	?	?	1	1	2	0	b	1	1	1	1	1	1
Scarrittia canquelensis	1	1	0	2	1	?	0	1	1	2	0	2	1	1	1	1	1	1
Anayatherium ekecoa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anayatherium fortis	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Huilatherium pluriplicatum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colpodon propinquus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Colpodon antucoensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchippus equinus	?	1	1	1	1	0	?	?	1	1	1	2	1	1	1	1	1	1
Rhynchippus pumilus	?	?	?	?	?	0	2	?	1	1	1	2	1	1	1	1	1	1
Argyrohippus fraterculus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Eurygenium pacegnum	1	?	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Nesodon imbricatus	1	1	1	2	0	0	2	1	1	1	1	2	1	1	1	2	1	1
Adinotherium ovinum	1	1	1	2	0	0	2	?	1	1	1	2	1	1	1	2	1	1
Homalodotherium cunninghami	1	?	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Federicoanaya sallaensis	0	?	0	?	?	0	1	1	1	1	1	1	1	1	0	0	0	0
Protypotherium australe	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0
Hegetotherium mirabile	?	?	?	1	1	0	1	0	0	0	0	0	1	0	0	0	0	1
Trachytherus alloxus	1	1	0	1	1	0	0	0	0	0	0	0	a	0	0	0	0	1
Mesotherium cristatum	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1

APPENDIX 2

Notoungulate taxa, references consulted, and specimens used for the phylogenetic analysis

OUTGROUP NOTOUNGULATE

Colbertia magellanica (Price and Paula Couto, 1950): Bergqvist and Fortes Bastos, 2009

ISOTEMNIDAE

Anisotemnus distentus Ameghino, 1902: Upper dentitions AMNH 5604 (cast); lower dentition AMNH 28696; postcrania Shockey and Flynn, 2007

Thomashuxleya externa Ameghino, 1902: Simpson, 1967; Shockey and Flynn (2007); Additional dental data obtained from AMNH 286447, AMNH 28649, an unworn M1)

HOMALODOTHERIIDAE

Homalodotherium cunninghami Flower, 1872: Flower, 1874; Scott, 1912b, 1930; Riggs, 1937

HEGETOTHERIIDAE

Hegetotherium mirabile Ameghino, 1887: Sinclair, 1909

INTERATHERIIDAE

Protypotherium australe Ameghino, 1887: (Sinclair, 1909, and various specimens in AMNH collection)

Federicoanaya sallaensis Hitz et al., 2008: Shockey and Anaya, 2008

Trachytherus alloxus Billet et al., 2008: Shockey et al., 2007

"NOTOHIPPIDS"

Eurygenium pacegnum Shockey, 1997: Shockey and Anaya, 2008

Rhynchippus equinus Ameghino, 1897: Loomis, 1914; additional data from FMNH P 13410

Rhynchippus pumilus Ameghino, 1897: Simpson, 1932; AMNH 29579; AMNH 29555

Argyrohippus fraterculus Ameghino, 1901: Simpson, 1932, and AMNH 29731 and FMNH P 13587

TOXODONTIDAE

Nesodon imbricatus Owen, 1846: Scott, 1912a, and various specimens in AMNH collection

Adinotherium ovinum Ameghino, 1887: Scott, 1912a, and various specimens in AMNH collection

LEONTINIIDAE

Anayatherium ekecoa Shockey, 2005

Anayatherium fortis Shockey, 2005 (restudy of repaired holotype UATF-V-00134; UF 225743, distal femur)

Ancylocoelus frequens Ameghino, 1895: Patterson, 1934; FMNH P 13348 and P 13496; AMNH 14493

Colpodon propinquus Burmeister, 1891 (= *C. distinctus*, but see Ribiero et al., 2010): Patterson, 1934; AMNH 14497 (cast); and AMNH 29721; FMNH P 13310, P 13304

Coquenia bondi Deraco, Powell, and Lopez, 2008

Huilatherium pluriplicatum Villarroel and Guerrero, 1985: Villarroel and Colwell Danis, 1997

Leontinia gaudryi Ameghino 1895: Ameghino, 1897; Loomis 1914; Patterson, 1934a; and FMNH P 12683, P 12684 P 13419, P 13463, P 13464)

Martinmiguelia fernandezi Bond and Lopez, 1995

Scarrittia canquelensis Simpson, 1934: Chaffee, 1952; AMNH 29585, manus and pes; AMNH 29626, tarsals; various specimens in AMNH collection

Taubatherium paulacoutoi Soria and Alvarenga, 1989: Paula Couto, 1983; and UF 225209, cast of MNRJ 4113-V

APPENDIX 3A

Summary data of radiometric analyses of ash sample SB55-32 CH-31 from the lower horizons of Cura-Mallín Formation, Laguna del Laja

T	t	40(mol)	40/39	38/39	37/39	36/39	K/Ca	Σ ^{39}Ar	^{40}Ar*	Age (Ma)
700	12	1.0e-15	7.6186	0.0e+0	19.4207	0.0183	0.025	0.00648	0.289	22.0 ± 7.1
770	12	1.5e-15	4.2960	0.0e+0	25.2823	0.0076	0.019	0.02346	0.475	20.4 ± 2.8
840	12	2.5e-15	3.1078	4.1e-4	30.3273	0.0033	0.016	0.06245	0.686	21.3 ± 1.3
910	12	3.6e-15	2.9205	0.0e+0	31.5325	0.0028	0.016	0.12104	0.715	20.9 ± 0.9
980	12	4.5e-15	2.6911	8.1e-5	31.7731	0.0021	0.015	0.20205	0.771	20.8 ± 0.7
1050	12	5.9e-15	2.9175	0.0e+0	31.6044	0.0028	0.016	0.29929	0.712	20.8 ± 0.6
1120	12	5.6e-15	2.6715	0.0e+0	31.0723	0.0021	0.016	0.40047	0.763	20.4 ± 0.6
1180	12	5.2e-15	2.9719	0.0e+0	30.2049	0.0029	0.016	0.48427	0.715	21.3 ± 0.7
1240	12	5.5e-15	3.6115	0.0e+0	29.6407	0.0048	0.017	0.55754	0.605	21.9 ± 0.8
1300	12	1.1e-14	5.0958	0.0e+0	29.6243	0.0091	0.017	0.65937	0.474	24.2 ± 0.6
1360	12	1.6e-14	4.5098	0.0e+0	30.5936	0.0071	0.016	0.82911	0.536	24.2 ± 0.4
1420	12	1.6e-14	4.4521	0.0e+0	30.7352	0.0070	0.016	1.00000	0.533	23.7 ± 0.4

Total fusion age, TFA = 22.32 Ma.
Weighted mean plateau age, WMPA= 20.82 ± 0.60 Ma (including J).
Inverse isochron age =19.25 ± 1.22 Ma. (MSWD = 0.24; ^{40}Ar/^{36}Ar = 358.0 ± 5.3).
Steps used: 840, 910, 980, 1050, 1120, 1180, 1240, 1300, 1360, 1420, (3–12/12 or 98% Σ ^{39}Ar.
t = dwell time in minutes.
40(mol) = moles corrected for blank and reactor-produced 40.
Ratios are corrected for blanks, decay, and interference.
Σ^{39}Ar is cumulative, ^{40}Ar* = rad fraction.
J = 0.0055792

APPENDIX 3B

Summary data of radiometric analyses of ash sample SB55-33 CH-32 from the lower horizons of Cura-Mallín Formation, Laguna del Laja

T	t	40(mol)	40/39	38/39	37/39	36/39	K/Ca	Σ ^{39}Ar	^{40}Ar*	Age (Ma)
700	12	1.5e-14	2.4934	0.0e+0	1.6805	0.0023	0.29	0.06265	0.725	18.0 ± 0.1
770	12	1.2e-14	2.2847	0.0e+0	3.2742	0.0014	0.15	0.11503	0.821	18.7 ± 0.1
840	12	1.7e-14	2.3406	0.0e+0	5.0417	0.0011	0.097	0.19016	0.856	19.9 ± 0.1
910	12	2.0e-14	2.3333	0.0e+0	5.9061	0.0010	0.083	0.27614	0.871	20.2 ± 0.1
980	12	2.0e-14	2.3234	0.0e+0	6.3356	0.0010	0.077	0.36397	0.875	20.2 ± 0.1
1040	12	1.5e-14	2.3455	0.0e+0	6.4322	0.0012	0.076	0.42990	0.843	19.7 ± 0.1
1100	12	1.1e-14	2.3904	0.0e+0	6.3930	0.0013	0.077	0.47532	0.840	20.0 ± 0.2
1160	12	9.1e-15	2.5633	0.0e+0	6.1892	0.0019	0.079	0.51154	0.787	20.1 ± 0.2
1220	12	8.2e-15	3.1626	1.2e-4	6.3919	0.0035	0.077	0.53802	0.677	21.3 ± 0.3
1280	12	2.7e-14	3.9458	0.0e+0	7.2567	0.0054	0.068	0.60829	0.596	23.4 ± 0.2
1340	12	6.6e-14	3.4976	0.0e+0	7.4519	0.0040	0.066	0.80040	0.662	23.0 ± 0.1
1400	12	6.5e-14	3.3032	0.0e+0	7.5353	0.0034	0.065	1.00000	0.693	22.8 ± 0.1

Total fusion age, TFA = 21.25 Ma.
Weighted mean plateau age, WMPA= 20.10 ± 0.12 Ma (including J).
Inverse isochron age =19.53 ± 0.60 Ma. (MSWD = 2.68; ^{40}Ar/^{36}Ar = 340.9 ± 22.6).
Steps used: 840, 910, 980, 1040, 1100, 1160, 1220, (3–9/12 or 42% Σ 39Ar.
t = dwell time in minutes.
40(mol) = moles corrected for blank and reactor-produced 40.
Ratios are corrected for blanks, decay, and interference.
Σ^{39}Ar is cumulative, ^{40}Ar* = rad fraction.
J = 0.0055517

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